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THE LATE MIOCENE ONGEVA LOCAL FAUNA OF CENTRAL AUSTRALIA.

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ABSTRACT

The late Miocene Ongeva Local Fauna (LF), comprising vertebrate remains derived from channel sands in the Waite Formation (Alcoota Station, central Australia), probably resulted from natural attrition around permanent or semi-permanent pools in seasonally flowing streams. Mortality due to prolonged drought, such as that postulated for the stratigraphically lower Alcoota LF, is not indicated. Strata hosting the Ongeva LF show more proximal fluvial characteristics than those hosting the Alcoota LF. Coarsening upwards in the section may be related to tectonism or climate change. New material of *Kolopsis yperus* Murray, Megirian and Wells (Zygomaturinae) makes more likely the possibility of its synonymy with *Zygomaturus gilli* Stirton (Cheltenhamian Stage of Victoria). Hypotheses of the phylogenetic position of these taxa within the Zygomaturinae seem reasonably stable, but it is observed that current taxonomy does not satisfactorily codify what is known of zygomaturine evolution. The Ongeva LF also contains *Kolopsis torus* Woodburne (previously known only from the Alcoota LF) and an undetermined species of the crocodylid genus, *Quinkana* Molnar.

KEYWORDS: Miocene, vertebrate palaeontology, Waite Formation, central Australia, Ongeva Local Fauna.

INTRODUCTION

Murray, Megirian and Wells (1993) provided the initial description and definition of the late Miocene Ongeva Local Fauna (LF) from Alcoota Station, central Australia, outlining its stratigraphic setting and biochronological significance of the zygomaturine diprotodontid *Kolopsis yperus*. Other components of the fauna were listed, but not described. Here we describe additional specimens of *K. yperus*, confirm the presence of *Kolopsis torus* Woodburne, and describe material referrable to the crocodylid *Quinkana* Molnar.

The accumulated sample of *K. yperus* upper third premolars morphologically encompass *Zygomaturus gilli* Stirton, raising the possibility of synonymy. However, an informative upper first molar of *Z. gilli*, important for establishing or refuting conspecificity with *K. yperus*, is lacking. The systematic position of these taxa within the Zygomaturinae, and taxonomic implications, are considered. A major component of the Local Fauna, the giant, flightless birds of the family Dromornithidae, are reserved for a future paper, but preliminary analyses suggest continuity with Alcoota LF taxa in the form of a *Dromornis* sp. cf. *stirtoni* and an *Ilbandornis* sp.

Although the accumulated Ongeva LF sample is small, and taxonomic work is incomplete, five years of collection has produced sufficient data to establish the general nature of the assemblage, which can now be compared with that of the underlying Alcoota Local Fauna. Observations of the stratigraphy and sedimentology of the Waite Formation in its type area are related to the regionally-focussed investigations by Senior *et al.* (1995) of the Tertiary intermontane basins of central Australia.

In Murray *et al.* (1993) we used the dental terminology of Archer (1978), under which diprotodontid cheekteeth are designated P3, M2 - M5. Here we revert to the older convention of P3, M1 - M4. A second Ongeva quarry was opened after the drafting of Murray *et al.* (1993). The original quarry on the north side of Hill 1 featured is Murray *et al.* (1993) is now distinguished as the 'Type Quarry', and the newer one on the opposite side of the hill is referred to as the 'South Quarry'.

Abbreviations. NTM, Northern Territory Museum; SGM, Spencer and Gillen Museum (now Museum of Central Australia), Alice Springs, Northern Territory. It is implicit where no institutional prefix is given that the material is lodged with NTM. TS refers to petrographic thin-sections at NTM.

STRATIGRAPHY, SEDIMENTOLOGY AND TAPHONOMY

Geological setting. The Waite Basin (Fig. 1) is one of many generally elongate structures filled with Cainozoic sediments within and surrounding the crystalline, Early to Late Proterozoic Arunta Block. The formations within these basins are broadly similar in their sedimentology, stratigraphy and alteration by weathering events, reflecting a similar geological history (Senior *et al.* 1995).

In general terms, a deep weathering event in the late Cretaceous was followed by a long period of predominantly lacustrine sedimentation lasting into the late Eocene. Two episodes of deep weathering affected these early Tertiary sediments, one in the pre mid-Eocene, and one in the late Eocene. There are also weak indications of the late Oligocene deep weathering event that affected adjacent parts of the continent, but otherwise non-deposition characterised the late Eocene to early Miocene, when predominantly fluviatile sedimentation commenced. Shifts in the drainage systems in the Oligocene or early Miocene were possibly due to uplift related to compressional tectonics resulting from the collision of the Australian and Pacific plates in the New Guinea region. This may account for the absence of a well-developed late Oligocene weathered profile in the region. The early Miocene to Holocene record is characterised by discontinuous fluviatile sedimentation, interspersed with more localised erosional

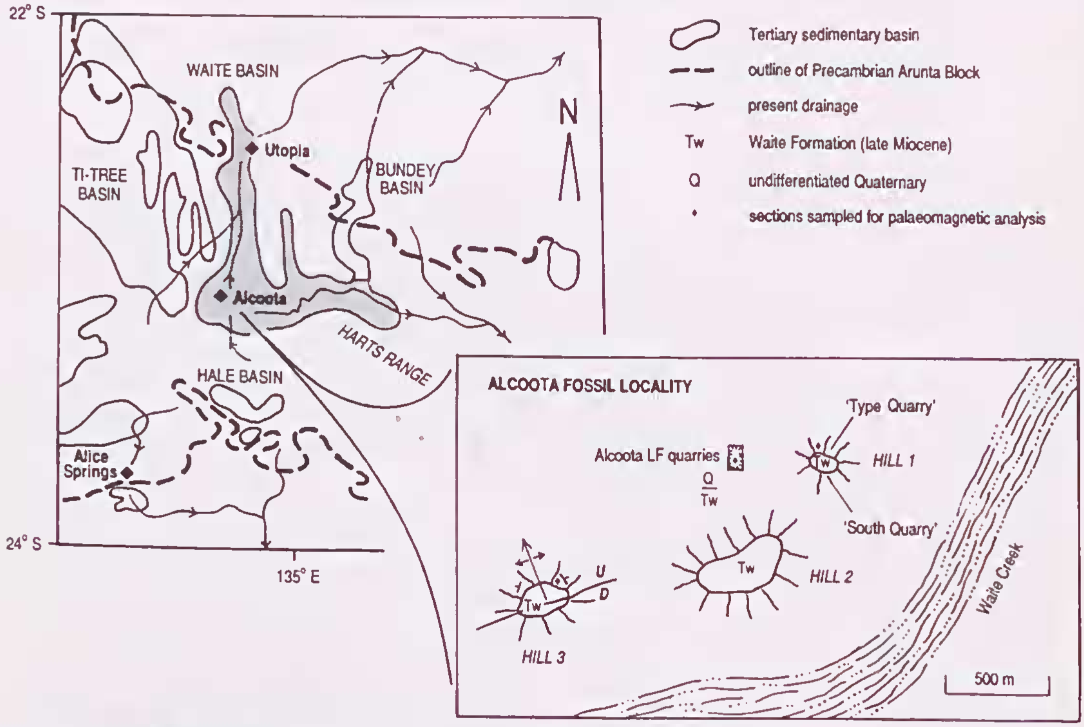

Fig. 1. Locality diagram after Senior *et al.* (1995: fig. 1) and Woodburne (1967a: fig. 2).

and weathering phases. There is also evidence of stream rejuvenation and changes in drainage patterns possibly related to minor tectonism. The later part of the sedimentary record (latest Pliocene onwards) contains aeolian sediments.

Sediments filling the Waite Basin are known informally as the Alcoota beds: those exposed in outcrop were formalised as the Waite Formation by Woodburne (1967a) (Senior *et al.* 1995). The composite thickness of the Alcoota beds is inferred to be about 250 m. The Waite Formation accounts for about 44 m, or 15%, of the Alcoota beds. It crops out at the southern periphery of the basin as interbedded chalcedonic calcarenitic limestone, sandstone, siltstone, and minor sandy conglomerate, and shows an overall pattern of coarsening upwards. The Waite Formation contrasts with the argillaceous Alcoota beds encountered in drill holes. Only a few metres of finer Alcoota beds, attributed to lacustrine sedimentation, are exposed as Waite Formation.

Stratigraphy. Quarrying on the north and south sides of Hill 1 between 1992 and 1995 provided better exposures of the stratigraphic succession hosting the Ongeva Local Fauna than were available to Murray *et al.* (1993), permitting some additional differention of sedimentary units. The elaboration presented below does not change the substance of the biochronological or biostratigraphic relationships of the Alcoota and Ongeva Local Faunas presented in Murray *et al.* (1993). To aid description, five informal lithostratigraphic members are recognised on Hill 1, designated I to V.

The stratigraphy of the South Quarry is shown in Figure 2. At the base is a pisolitic unit (I), which forms the floor of the quarry. Ferrugi-

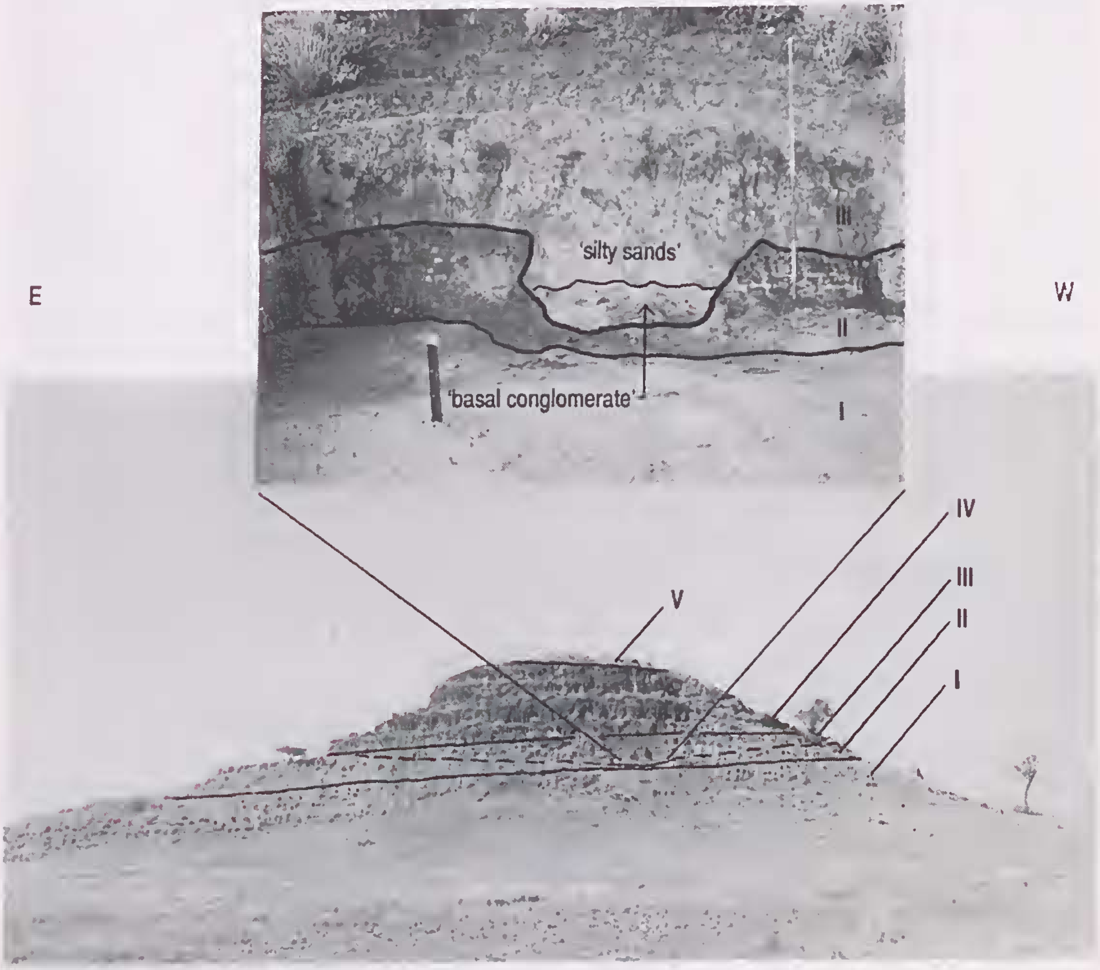

Fig. 2. Hill 1 from the south, and stratigraphy in the 'South Quarry', July, 1995. Divisions on the stadia rod in the quarry are 0.5 m. The hillslope above the 1.5 m mark on the stadia rod has been cleared of loose boulders and benched. Informal members I - V as described in the text.

nous pisolites and their sandy silt matrix are cemented by diagenetic calcite to form a competent rock (Fig. 3A, B). This unit, described more fully in Murray *et al*. (1993), represents an ancient weathered profile, and its surface is the major unconformity separating strata hosting the Ongeva and Alcoota Local Faunas.

The pisolitic unit is succeeded in sharp, but irregular, contact by an unfossiliferous ferruginised and calcified unit, which in textural terms is a poorly sorted, silty sandstone (II) (Fig. 3A). The coarse fraction consists mostly of quartz, with ironstone and other lithic grains comprising a minor component, set in a ferruginous matrix. The grains range from sub-angular to rounded. No sedimentary structures are evident. Within the quarry, the unit has a massive appearance, due to the fairly homogenous degree of iron induration, but the distribution of the coarse clastic fraction varies laterally and vertically. The ferruginisation is attributable to both staining of finer clastic particles (silt size) and ferruginous cement, which together form the matrix of the unit. Diagenetic sparry calcite

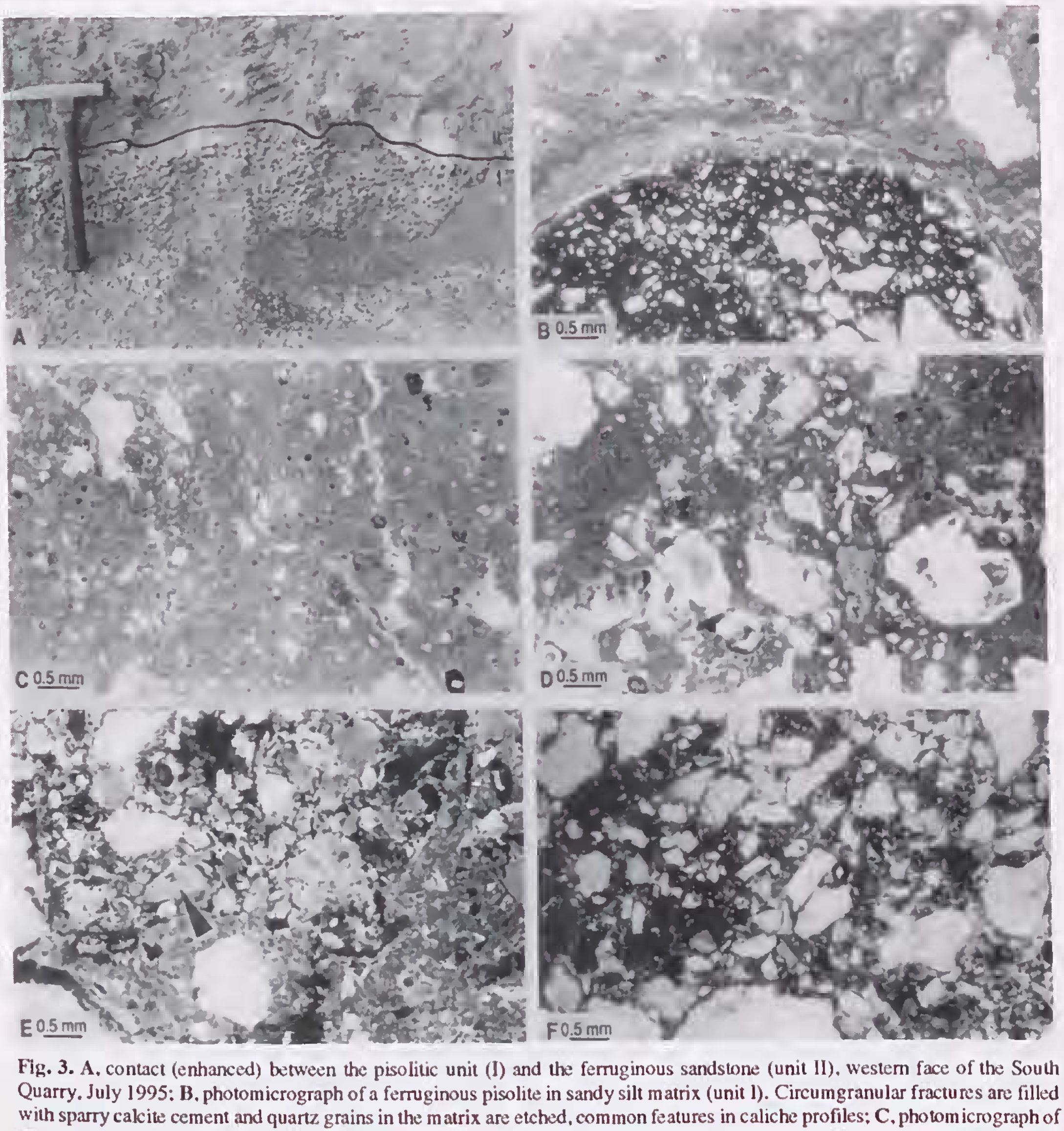

Fig. 3. A, contact (enhanced) between the pisolitic unit (I) and the ferruginous sandstone (unit II), western face of the South Quarry, July 1995; **B**, photomicrograph of a ferruginous pisolite in sandy silt matrix (unit I). Circumgranular fractures are filled with sparry calcite cement and quartz grains in the matrix are etched, common features in caliche profiles; **C**, photomicrograph of sandy silt bed (unit III), Type Quarry; **D**, photomicrograph of silty sand (unit III), Type Quarry; **E**, photomicrograph of silty sand with bone shards (unit III), South Quarry; **F**, photomicrograph of red sandstone (unit IV). B, C, D and F in plane polarised light; E crossed polars.

is also present in veins. Along strike, outside the quarry to the west and around to the opposite side of the hill, weathered outcrop is much lighter in colour (very pale orange). The unit was probably initially deposited as poorly sorted silty sandstone, similar to those comprising higher units on Hill 1, diagenetically altered to a duricrust (ferricrete / calcrete) during an episode, or episodes, of sub-aerial exposure. Additional evidence for a hiatus comes from the erosional unconformity with the succeeding fossiliferous (Ongeva Local Fauna) sediments (III).

In the South Quarry, the Ongeva Local Fauna beds (III) are confined at their base to a narrow, steep-sided channel, about 1.5 m wide and 0.5 m deep (Fig. 2). The western bank of the channel is undercut, while the eastern bank has an apparent slope of about 60°. The steep bank profiles indicate that the fossiliferous beds were deposited over a unit already stabilised to a high degree of mechanical competence before channel incision. The base of the channel contains a 10 to 20 cm thick conglomerate, composed of pebble- to cobble-sized crystalline metamorphics, vein quartz, ferricrete clasts, cream to pale greeen calcareous siltstone and sandstone, ferruginous pisolites, and vertebrate fossils (described separately below). Interstices between the large clasts are filled with white to pale green calcareous siltstone, with some primary intergranular porosity filled with diagenetic coarse, sparry calcite cement. The crystalline igneous and metamorphic rocks were derived from the basement complex of the Waite Basin, the ferricrete clasts and pisolites probably reworked from the two underlying units (I and II), and the calcareous lithoclasts are probably intraformational reworkings (i.e. lithofacies of unit III).

The basal conglomerate of unit III is succeeded by poorly indurated, pale greenish yellow, bedded, silty sand (Fig. 3E). The higher exposures of the unit in the South Quarry are affected by ferruginous mottling, which penetrates with decreasing intensity to about 1.5 m below the present land surface. Un-mottled material was only intersected at the back of the quarry (Fig. 2). Faintly visible through the mottling are bedding traces. The lowest bed fills the channel and extends over the banks, reaching a maximum thickness of about 1.2 m over the basal conglomerate. The succeeding beds are thinner (20 - 30 cm). The top of the unit and its contact with the overlying, dark red, unfossiliferous conglomeratic sandstones (IV) is not clearly exposed, but the maximum thickness of the fossiliferous unit is in the order of 2 m. The sand and grit fraction consists of angular to rounded quartz, crystalline lithic grains and minor plagioclase. Excluding the large bones and bone fragments, the lowest bed is significantly bioclastic, containing bone shards up to 10 mm long. The distribution of these is variable in the quarry, from being a trace component up to an estimated 5% of the volume. The bone shards, especially ones composed of compact bone, resemble fragments resulting from sub-aerial weathering after the collagen is broken down.

The unfossiliferous red silty sandstones and minor interbedded conglomerates (IV) of Hill 1 are composed of poorly sorted angular quartz, lithic grains, plagioclase and microcline feldspars, and weathered mica (?muscovite) (Fig. 3E). They contain less fines, and are indurated to a greater degree than the underlying beds, which together with their compositional and textural immaturity, reflect a change in the sedimentological regime. The contact between units III and IV coincides with Woodbume's (1967a) subdivision of the Waite Formation into two (informal) members, the lower 'lacustrine beds' and the upper 'fluviatile beds'. The top of Hill 1 is occupied by residual boulders of chalcedony (V), the last remnants of a bed of pedogenic limestone, as described in Woodburne (1967a).

The stratigraphy within the Type Quarry is similar to that in the South Quarry, differing only in that within unit III, the basal conglomerate and silty sandstones are separated by a thin (c. 20 cm) unit of sandy silt (Figs 3C, 4). This may be equivalent, at least in part, to the matrix of the conglomerate in the South Quarry. The contact between the silty bed and the superposed coarser lithologies (Fig. 3D) is distinct, but irregular. The fossiliferous sediments are not as confined as they are in the South Quarry. The western bank of the channel is lower and more gently inclined than on the opposite side of the hill. The eastern bank remains hidden below scree, so that the full width of the channel cannot yet be determined. However, it is greater, though perhaps not much more so, than the 8 m width exposed in the quarry: the lenses of channel-fill, evident through the mottling, are lowest mid-way along the quarry face (Fig. 4).

The sandstone (II) into which the Ongeva Local Fauna beds are incised was not inter-

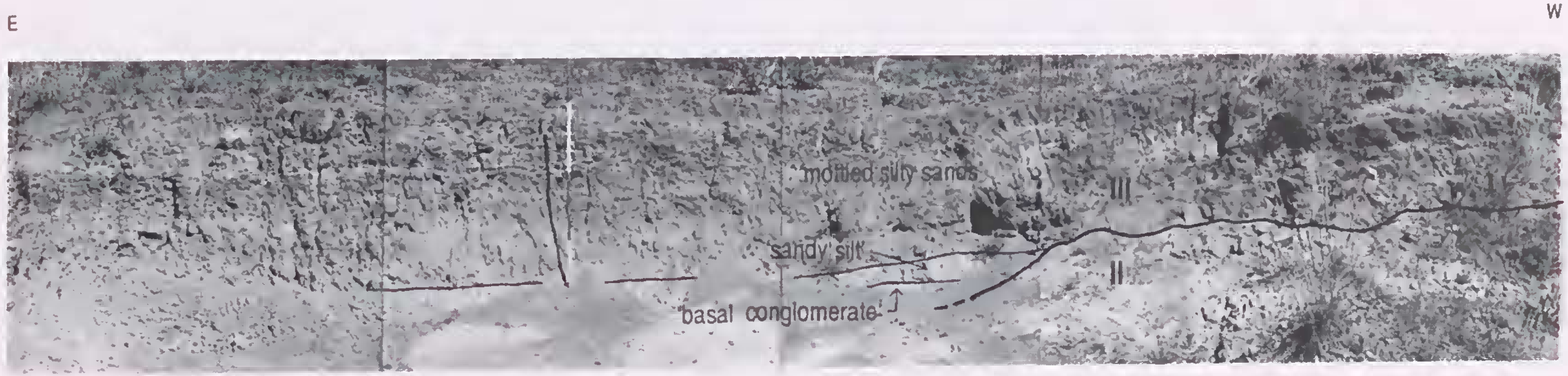

Fig. 4. Photomosaic of the Ongeval LF 'Type Quarry' (July, 1995 - the quarry was last worked in July, 1994). Colluvium shed from the quarry face in the year preceding photography obscures most of the 'basal conglomerate' and 'sandy silt' of unit III, which terminate against unit II at the western edge of the quarry. Lenses of silty sand (III) are discernible through mottling. Divisions on the stadia rod are 0.5 m. The hillslope above the quarry (above the 1.5 m level on the stadia rod) has been cleared of loose boulders and benched.

sected in the section logged by Murray *et al.* (1993: fig. 2), a few metres east of what is now recognised as the western bank of the channel. The appearance in outcrop of these two sedimentary units differs from their exposures below the zone of weathering apparently related to the present land surface. This current phase of weathering has resulted in the mottling of unit II and a lightening in colour of unit III, which might be due either to surficial leaching of iron, or more likely, a lighter overprint of calcrete. Consequently, the two units have a similar appearance in outcrop and shallow subcrop. Because of this similarity, coupled with inadequate exposure, Murray *et al.* (1993: 158) interpreted the silty bed of unit III as being continuous with what is here differentiated as unit II:

> .. the contact between the two [the sandy silt bed and the lowest silty sand bed of unit III] is irregular, and where it can be traced from the [Type] quarry along strike to a point about 10 m to the west, has a relief of about 0.8 m.

The margin of the Type Quarry was then a few metres east of its position in 1994/95, but as Figure 4 shows, while the contact between sandy silt and the silty sand beds is irregular, the sandy silt terminates in the channel against unit II, and its contact with the silty sand has no such relief. Woodburne's (1967a) description of his member 5 in the Hill 1 section appears to include attributes of both units II and III. He measured his section on the southwestern face of the hill (where unit II crops out), but noted that 'sparse fossils (occur) as weathered fragments in more reduced pockets .... on the northwest face of the hill' (Woodburne 1967a: 175).

The fossiliferous beds (III), being notably less indurated, weather recessively and are almost entirely covered by scree, while the duricrusted host sandstone (II) crops out as a resistant ledge at the eastern end of Hill 1, as does the underlying pisolitic unit (I) (Fig. 2). The sharp and irregular contact, and the lithological differences, indicate that unit II is not genetically related to the pisolitic unit (I). Unit II was deposited unconformably on Unit I, and then duricrusted during a phase or phases of subaerial exposure, the effects of which may have penetrated into unit I, overprinting earlier diagenesis. The stratigraphy of Hill 1 is summarised in Figure 5. The interpretation of two palaeo-surfaces between Alcoota and Ongeva Local Fauna times merely reinforces the chronostratigraphic separation of the two assemblages.

No sedimentary structures were observed in unit III in either quarry that indicates the direction of sediment transport. The similar north-south channel alignments observed in both quarries, similar base level, and approximately 40 m horizontal separation, indicates that the same channel or confluent channels are intersected in the two quarries. The contrasting cross-sectional proportions, narrow and deep in the South Quarry, and shallow and wide in the Type Quarry, suggests that across the width of Hill 1, the palaeohydraulic gradient was from south to north.

In an endeavour to more completely characterise the stratigraphy, and perhaps even the age, of the Waite Formation in the Alcoota area, Hill 1, Hill 3, and the strata exposed in the Alcoota Local Fauna quarries, were sampled during 1992 for palaeomagnetic analysis (Fig.1). The type section of the formation at Hill 2 was not selected because weathering is deeper and more advanced than in other sections, and consequently offered weaker prospects for useful results. Samples were subjected to comprehensive alternating field (AF) and thermal demagnetisation. Demagnetisation quality was poor, and the results disappointing. All three sections sampled are dominated by normal magnetic polarities, with recorded NRM (Natural Remanent Magnetisation) intensities correlated to increased red (iron oxide) pigmentation upsection. It thus seems likely that the normal polarity directions are pedogenic overprints, rather than primary (M. Whitelaw, University of Texas, written communications, 20 March and 28 April, 1994).

Some of the beds sampled for palaeomagnetic analysis at Hill 3 dip at angles as high as 13° to the northeast. While the beds are lenticular, the unit which they comprise ('fluviatile beds' of Woodburne 1967a) was traced in outcrop to the west, where beds dip northwest, though at lower angles (2-4°). It is difficult to attribute the divergent angles of dip to deposition. The observed attitudes of bedding at Hill 3 are consistent with a small anticlinal structure plunging to the north, with an axial plane dipping at a high angle to the west. The structure is exposed on the upthrown side of an east-west trending fault recorded by Woodburne (1967a) (Fig.1).

Taphonomy. No marked differences were noted in the palaeontology of the two Ongeva

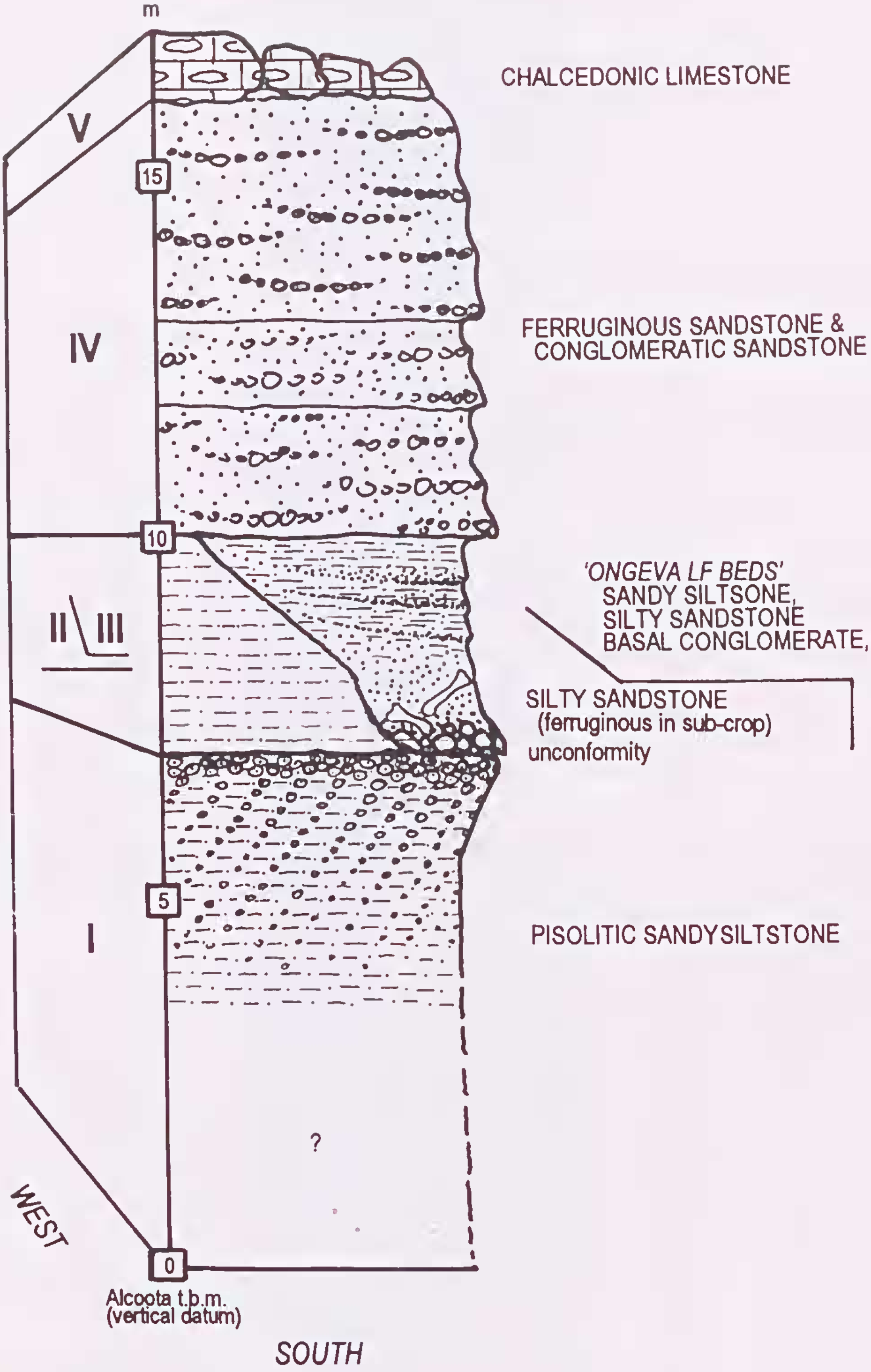

Fig. 5. Schematic diagram of the Waite Formation stratigraphy at Hill 1.

LF quarries. Due to the generally fragile condition of the fossils, not all specimens could be successfully extracted.

Remains of several species of large flightless birds (Dromornithidae) and large herbivorous marsupials (Zygomaturinae) predominate in the basal conglomerate (Fig. 6A). The dromornithids are mostly represented by the shafts of long bones (especially tibiotarsi and tarsometatarsi, less frequently femora). The long bones lie horizontally or sub-horizontally, aligned parallel or at low angles to the channel margins. Pes elements and other post-cranials, and cranial fragments are infrequent. Zygomaturinae are represented predominantly by disarticulated maxillae, horizontal rami of dentaries and long bones (usually with damaged ends). Other cranial and post-cranial fragments are less frequent. Ribs of the large avian and marsupial herbivores are represented only by short fragments. Fragmentary crocodile remains, and postcranials (mostly manus and pes elements) of a small macropodid (cf. *Dorcopsoides*) contribute to the smaller size fraction. Fossils from the basal conglomerate are typically well mineralised.

Fossils from the silty sand and sandy silt are similar in their taxonomy and representation, differing only in the following respects: broken edges of bones are generally less rounded and in some cases sharp; depositional orientations of long bones are random (some vertical); and few fragile skeletal elements are preserved. The lower beds have a greater concentration of bones than the higher beds, but more complete specimens occur at a higher frequency up-section. Mineralisation is generally poor, with the exception of the few collected from high in the mottled zone, where diagenetic emplacement of iron and possibly magnesium oxides has toughened them to a high degree.

In the 'Type Quarry', two coprolites (P9271, P9413) were found deposited directly upon bones embedded in the basal conglomerate. Both coprolites resemble Recent cow pats in their size and gross morphology (Fig. 6B). Preservation is attributable to calcification. In sawn transverse section, P9413 is irregularly laminated

Fig. 6. A, four dromornithid long bones, from left to right, cf. *Dromornis* femur and tibiatarsus, cf. *Ilbandornis* tibiatarsis, and cf. *Dromornis* tibiatarsus, all lacking ends and showing a preferential alignment to the channel margins as indicated by the compass, in the basal conglomerate of the South Quarry. The tooth row of *K. yperus* (P961) is exposed in the centre of the upper right quadrant; B, a coprolite (P9271), *in situ* in the 'Type Quarry' (July 1992), with a Recent cowpat (bottom centre) for comparison; C, transverse slab through coprolite P9413; D, photomicrograph (TS 0084) of coprolite P9413 in plane polarised light.

(Fig. 6C). Thin sections (Fig. 6D) show alveolar to clotted texture. Fabric elements include microspar, tubular root moulds, peloids, glaebules defined by circumgranular fractures, and clay cutans. Fractures and root moulds are filled with sparry calcite cement, though in some instances, geopetal carbonate silt occupies the lower part of voids. There are also signs of incipient silicification as chalcedony. Many of these internal features are characteristic, and some diagnostic, of caliche (e.g. Estaban and Klappa 1983). Post-depositional processes in an environment conducive to pedogenic carbonate emplacement thus appears to have both fossilised the coprolites and completely obliterated original internal structures and fabrics, leaving no clues as to the plant matter that was consumed by the animals leaving these traces, or its state after digestion, though it was most probably very finely divided.

Thus, remains of dead animals accumulated, most likely by natural attrition, within the catchment of a small, probably ephemeral stream. Only the larger and most robust skeletal elements became preserved locally as components of the channel lag (basal conglomerate). The remainder were swept downstream, to be deposited at some unknown location. The length of time over which these typically eroded fossils, representing a highly winnowed fraction, were accumulated is unknown, but perhaps over a considerable period, during which they became both (syndepositionally) mineralised and cemented into place.

A transition in sedimentological regime is indicated by the channel filling sediments. Deposition of the lowest Ongeva LF bed, a sandy silt restricted to the downstream segment of the channel, buried the coprolites deposited by large herbivores without displacing them. A subsequent, more energetic event mobilised large amounts of sediment and the skeletal remains which had accumulated, still by natural attrition, within the catchment. Some bones had laid on the surface for some time before transportation, extended sub-aerial exposure permitting both scavenging, disassociation, trampling, and physico-chemical denaturing and disintegration of the bones. The detritus was swept into the channel and deposited as poorly sorted silty sand, incorporating large bones and bone fragments in random orientations. The high sediment load limited the capacity of the stream to deeply scour and rework the underlying sandy silt, or to sort its load.

The channel continued to aggrade with similar deposits, but these depositional events occurred with a frequency that allowed little time for skeletal elements to accumulate in the catchment, as evidenced by the decreasing frequency of vertebrate fossils, but generally more complete specimens, up-section.

SYSTEMATIC PALAEONTOLOGY

Diprotodontidae Gill
Zygomaturinae Stirton, Woodburne and Plane
Kolopsis torus Woodburne, 1967b

(Tables 1-3)

Referred material. P92152, right dentary; P92153, left dentary; P92178, right dentary; P92147, edentulous right maxilla; P9216, left and right maxilla; P967, left dentary M_{2-5}; P968, right dentary M_{2-5}; P969 left dentary M_{2-5}; P9610, left premaxilla and maxilla, I^1, P^3, M^{2-5}; P9216, left and right maxillae.

Description. The Ongeva *Kolopsis torus* material, in so far as it is represented, conforms to the original diagnosis of the Alcoota Local Fauna sample of the species (Woodburne 1967a,b) and does not require additional description. A few measurements of the teeth fall outside the range of the Alcoota sample (Tables 1-2).

Comparative remarks. The Ongeva *Kolopsis torus* sample is structurally indistinguishable from the Alcoota sample, but shows some slight morphometric differences in the teeth. The small Ongeva sample size precludes any meaningful statistical comparisons with the Alcoota population, but we observe that the differences are probably no greater than those expected of a separate population sample of the same species.

Kolopsis yperus Murray, Megirian and Wells, 1993

(Figs 7-15, Tables 4-6)

Type material. Holotype SGM P92117, right P^3 and M^1.

Referred material. P9346, right maxilla fragment with P^3-M^{1-4}, P9236, left maxilla fragment with P^3-M^{1-2}; P961, left maxilla fragment with P^3-M^{1-4}; P962, left maxilla fragment with M^{3-4}; P963, right M^2; P9480, right M^1; P964, right I^1 root; P965, right maxilla with M^{3-4}; P9344, left

Table 1. Comparison of upper cheek teeth measurements of Ongeva LF *Kolopsis torus* compared with range of variability in Alcoota LF *K. torus*. Alcoota LF *K. torus* from Woodburne (1967b: Tables 8 and 9). **L** = length; **W** = width; **WP** = width protoloph; **WH** = width hypoloph.

		P^3		M^1			M^2			M^3			M^4		
		L	W	L	WP	WH	L	WP	WH	L	WP	WH	L	WP	WH
Ongeva															
P9216	L	17.0	14.5	16.6	16.2	17.0	19.7	18.7	19.0	21.5	20.6	19.5	22.0	-	-
	R	-	-	-	16.8	-	19.1	19.2	17.4	-	-	-	-	-	-
P9477		18.3	15.4	18.5	17.3	-	20.5	20.3	19.3	24.0	23.3	19.4	-	21.5	-
Alcoota															
Range		17.1-20.5	13.7-16.1	17.4-20.5	16.2-18.3	16.4-18.7	19.7-22.9	19.2-21.4	17.8-21.4	21.5-25.0	20.4-23.2	17.7-21.1	21.2 -25.3	20.1-23.3	14.8-22.0

Table 2. Comparison of lower cheek teeth measurements of Ongeva LF *Kolopsis torus* compared with range of variability in Alcoota LF *K. torus*. Alcoota LF *K. torus* from Woodburne (1967b: Tables 11 and 12). L = length; W = width; WP = width protolophid; WH = width hypolophid.

	P_3		M_1			M_2			M_3			M_4		
	L	W	L	WP	WH	L	WP	WH	L	WP	WH	L	WP	WH
Ongeva														
P92153	-	-	-	-	-	-	-	-	26.1	17.8	17.9	24.4	19.0	17.2
P92178	14.2	9.7	20.3	14.3	14.9	22.4	16.5	17.2	24.0	20.8	18.3	27.5	20.0	17.2
P92152	-	-	18.0	12.2	13.9	20.4	17.9	-	-	-	-	-	-	-
P9474	-	-	-	12.1	12.6	20.0	15.1	14.9	22.0	18.6	17.2	23.1	18.6	17.5
P9475	-	-	17.5	-	-	21.3	-	-	22.7	-	-	25.0	-	-
P9476	-	-	17.1	12.9	13.3	19.6	15.5	15.0	23.4	-	-	-	-	-
P9478	-	-	-	-	-	-	-	-	-	-	-	28.0	18.3	20.2
Alcoota														
Range	12.3-15.5	9.1-11.3	17.2-19.1	12.1-14.8	12.5-15.1	18.7-21.6	14.1-17.3	13.9-16.0	21.8-25.8	16.4-19.7	15.5-18.1	22.1-27.0	17.3-21.0	15.6-20.0

Table 3. Dimensions of the lower jaws of Ongeva LF *Kolopsis torus* compared to the range of variability in Alcoota LF *K. torus*. Alcoota LF *K. torus* data from Woodburne (1967b: Table 13).

	P92153	P92178	P92152	range in Alcoota LF *K. torus*
length of diastema	-	-	43	27.0 - 45.5
mandibular canal to postalveolar process	29	-	29	20.8 - 30.8
post alveolar process to posterior edge of M_4	21	-	-	8.5 - 21.8
depth of horizontal ramus below $M_{3/4}$	53	47	-	42.3 - 54.5
depth of horizontal ramus below $M_{1/2}$	46	45	-	39.2 - 50.9
depth of dorsal edge of jaw to mental foramen	-	13	-	15.2 - 21.8
anterior edge of P_3 to mandibular canal	149	-	-	140.5 - 152.5
anterior edge of P_3 to postalveolar process	129	121	-	118.1 - 136.4
length P_3 to M_4	105	111	-	100.0 - 113.7

dentary with M_{2-4}; P966, left dentary with M_{2-4}; P9223, left dentary with damaged tooth row, M_{2-3} and crushed horizontal ramus; P9344 right posterior part of horizontal ramus of dentary, lacking teeth.

Type locality. Alcoota Station, latitude 22°52'S, longitude 134°27'E. Specimens were recovered from two quarries located on the north and south sides of Hill 1. Both quarries intersect sandy channel deposits situated above an unconformity approximately 10 m above the fossiliferous lacustrine sediments containing the Alcoota Local Fauna.

Fauna. Ongeva Local Fauna.

Rock unit and age. Waite Formation, Cheltenhamian equivalent, late Miocene - early Pliocene.

Revised diagnosis. As given for *Kolopsis yperus* Murray, Megirian and Wells, 1993, with definition amended as follows: P^3 crown ranges from slightly smaller to considerably larger than that of the holotype *Zygomaturus gilli* Stirton, 1967; and, dentary symphysis fused and large genial fossae present.

Description. *Maxilla.* The four new fragments of facial cranium (Figs 7-10) confirm previous observations (Murray *et al.* 1993), based on less complete material, that the cranium of *Kolopsis yperus* lacks many of the specializations that characterize *Zygomaturus trilobus*. The lower margin of the orbit preserved in three specimens (P965, P9236, P961) indicates that the orbits are small, about 30.0 mm in diameter, with thick, rounded lower emarginations. The facial height measured from the inferior orbital margin to the interproximal crevice between the metastyle of M^1 and the parastyle of M^2 ranges from 40.0 mm in P9236 to 60.0 mm in P961.

In the mature specimens, a deep, elliptical suborbital fossa is developed, similar in size and shape to that of *Plaisiodon centralis* Woodburne. This structure is only slightly developed in the youngest individual (P9236). The rounded suborbital crest sweeps posteriorly at about a 45° angle relative to the palatal midline, giving rise posteriorly to the zygomatic process.

The zygomatic process is robust and expanded transversely in P965, being approximately 28.0 mm wide and 16.0 mm thick, with a strongly developed masseteric crest. In P9236, the less mature individual, the zygomatic process is small and compressed laterally. When complete, it would not have extended below the occlusal plane of the molars, whereas that of P965, although broken a considerable distance above its termination, extends more than 20.0 mm below the occlusal plane of the molars. In P965 a low, rounded postorbital eminence is present and the zygomatic root expands into a rounded boss at the confluence of the zygomatic process and base of the zygomatic arch.

Because of numerous cracks, the maxillojugal suture is not easily traced on any of the specimens. It appears to divide the zygomatic process into approximately equal parts in P965, whereas in P9236, the lateral 4/5 of the zygomatic process is formed within the jugal. The suture is clearly defined behind the orbital margin as a narrow crescentic cleft, and as it continues inferiorly it forms a low crest emarginating the lateral side of the suborbital fossa.

The alveolar shelf is narrow but very strongly accentuated by a sharp crest continuous with the internal border of the zygomatic process. The infraorbital canal is preserved on P965. It is located 27.0 mm posterior to the inside of the inferior orbital crest, The optic foramen opens 55.0 mm posterior to the inferior orbital crest. The height of the alveolar shelf ranges from 37.0 mm to 42.0 mm above the M^3/M^4 alveolar margin.

The palatal processes of the maxilla are about 8.0 mm to 12.0 mm thick near the median suture. The palatal surface is flat with shallow longitudinal grooves. The estimated width of the palate at M^3/M^4 is 65.0 mm (P965) and about 60.0 mm at P^3/M^1 (P961). P9346 preserves about 35.0 mm of the diastema. The diastemal crest is rounded and indistinct. A shallow nasolabial fossa is present anterior to the P^3 root.

Upper incisor. The right I^1 (P964) closely resembles the referred specimen NTM P92114 previously described by Murray *et al.* (1993) although it is slightly thinner in section, less curved and slightly less tapered proximally. The tip of the crown is either worn off or broken near the dentine-enamel junction. The specimen is plano-convex in section, being flat-surfaced mesially over its entire length. The maximum thickness of the root is 13.0 mm and approximately 25.0 mm deep anteroposteriorly. Its length along the dorsal margin is about 114.0 mm.

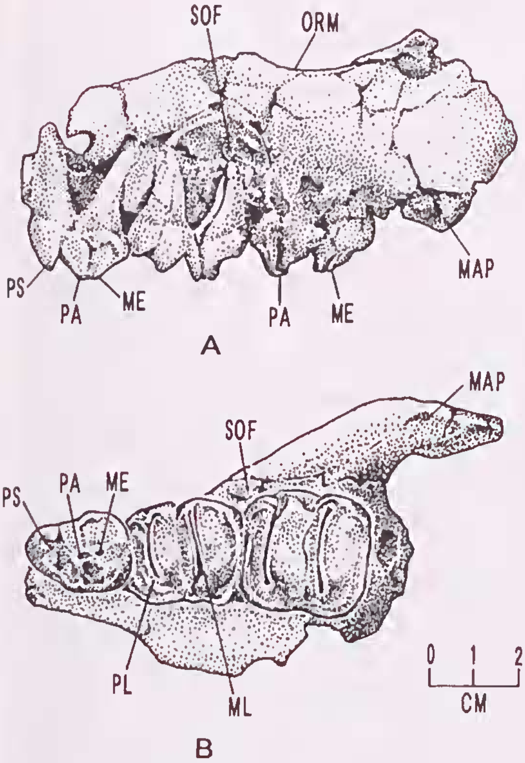

Fig. 7. Left maxilla fragment of a young *Kolopsis yperus* (P9236) in which the teeth show slight wear, the masseteric process is small and the suborbital fossa is scarcely developed; A, labial aspect; B, occlusal aspect. Abbreviations: **PS**, parastyle; **PA**, paracone; **ME**, metacone; **SOF**, suborbital fossa; **ORM**, inferior orbital margin; **MAP**, masseteric process.

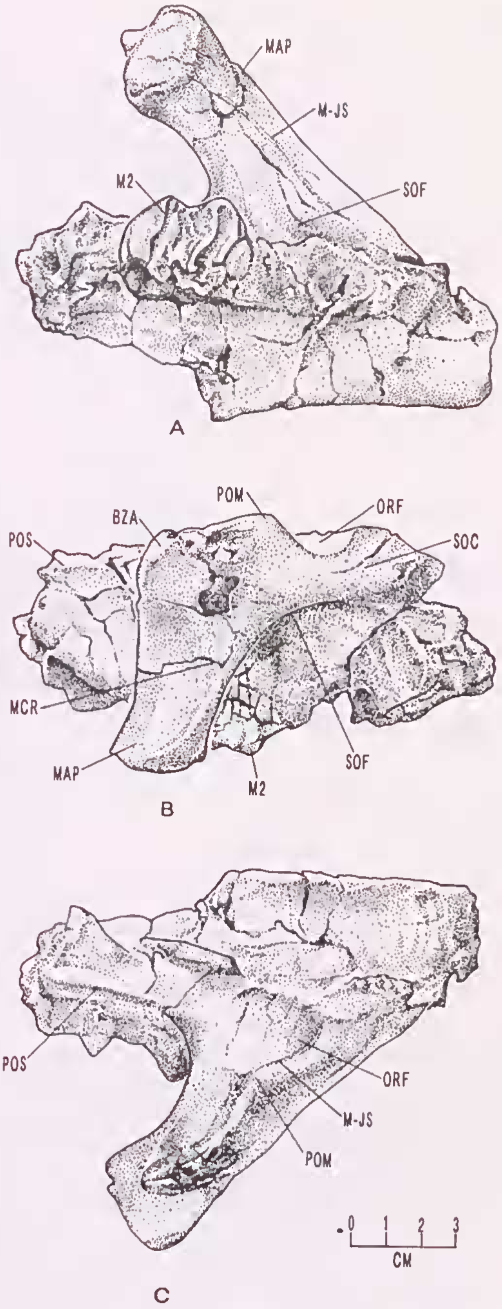

Fig. 8. Right maxilla of *Kolopsis yperus* (P963) preserving the lower margin of the orbit and part of the zygomatic process. The morphology of the orbit and "cheek" region of *Kolopsis yperus* closely resembles that of *Kolopsis torus* in basic shape and orientation; the orbit is open laterally and the suborbital crest trends obliquely posteriorly. Some partial resemblances to *Zygomaturus trilobus* are also present: the zygomatic process is large, wider transversely than anteroposteriorly, and the base of the zygomatic arch indicates a steep posterior orbital margin. A, palatal aspect; B, labial aspect; C, dorsal aspect. Abbreviations: **M2**, second upper molar (M^2); **MAP**, masseteric process; **MCR**, masseteric crest; **M-JS**, maxillo-jugal suture; **POM**, postorbital margin; **ORF**, orbital fossa; **POS**, postorbital shelf; **SOC**, suborbital crest; **SOF**, suborbital fossa.

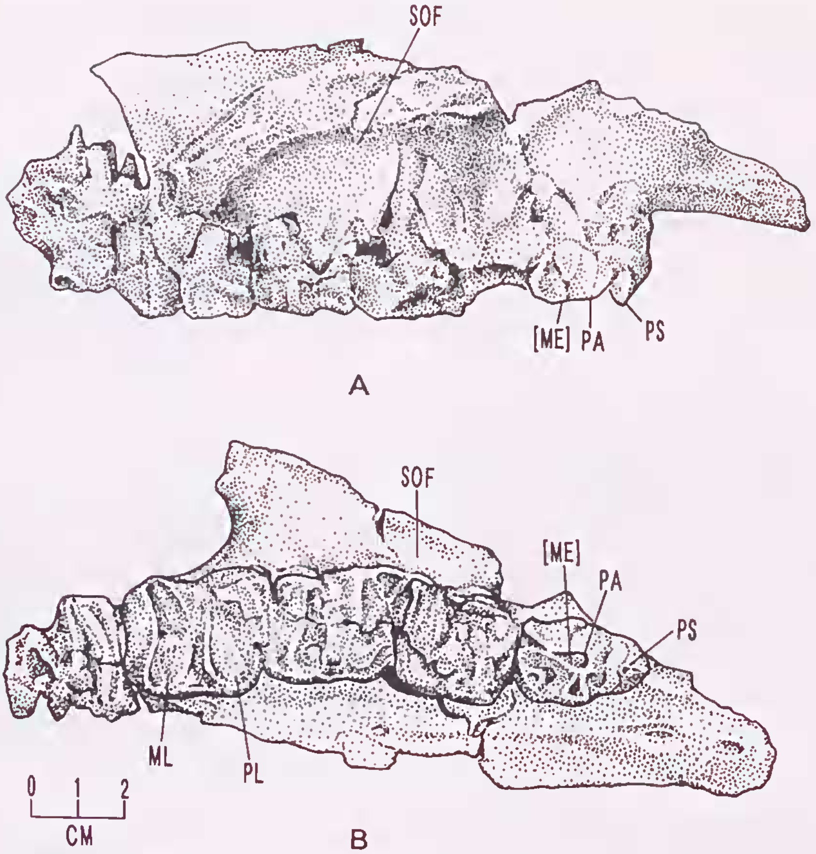

Fig. 9. Right maxilla fragment of *Kolopsis yperus* (NTM P9346). A, labial aspect; B, palatal aspect. Abbreviations: [ME], position of heavily worn metacone; ML, metaloph; PA, paracone; PL, protoloph; PS, parastyle; SOF, suborbital fossa.

Upper premolar. The four P^3 specimens of *K. yperus* are variable in size and outline shape, as characterizes the upper premolars of other taxa in the subfamily Zygomaturinae. The holotype *K. yperus* SGM P92117 is slightly smaller than that of the holotype of *Z. gilli*, whereas that of P9236 is nearly identical at 23.0 mm long and 17.8 mm wide. P961 is larger than the *Z. gilli* holotype (L=24.5 mm, W=20.4 mm) and that of P9346 is longer again (L=26.0 mm) though proportionally narrower (W=19.0 mm).

With the exception of P9346 which is heavily worn, all of the new specimens (Fig. 11) show clear differentiation of the paracone and metacone. They also express a large, transversely broad parastyle closely approximated to the paracone base, a short, strong posterolabial cingulum and variable mesostyle and a crest that ascends the labial side of the parastyle extending from the transverse commissure to the apex of the cusp.

NTM P9236 closely resembles the type specimen of *Z. gilli* in all essential morphological details. As the specimen (P9236) is only slightly worn, the crown height from the apex of the paracone to the enamel-dentine junction is 18.3 mm. It is therefore considerably higher-crowned in proportion to its length than that of *Kolopsis torus*. The transverse link between the paracone and the protocone is high and a small basin is formed on the anterolingual side of the parametacone which is partly enclosed posteriorly by the basal swellings of the hypocone and metacone. The hypocone of P9236 is nearly as large as the protocone. In *Z. gilli* the hypocone, which is a variably developed cusp in all zygomaturine species in which it is present, is small.

The parastyle is wider than long. A thick lingual crest ascends its apex. The labial crest is weaker. A thick, rounded preparacrista extends to the base of the parastyle from the apex of the paracone. The triangular paracone is much larger

Table 4. Upper cheek teeth measurements of *Kolopsis yperus*. L = length; W = width; WP = width protoloph; WH = width hypoloph.

	P^3		M^1			M^2			M^3			M^4		
	L	W	L	WP	WH	L	WP	WH	L	WP	WH	L	WP	WH
SGM P92117 (R)	21.5	17.1	24.3	21.2	21.2	-	-	-	-	-	-	-	-	-
P9236 (L)	23.0	17.8	24.4	21.5	22.7	27.0	25.0	24.6	-	-	-	-	-	-
P962 (L)	-	-	-	-	-	-	-	-	33.0	27.7	22.2	30.5	24.8	19.5
P961 (L)	24.5	20.4	23.0	22.7	23.3	27.0	26.1	24.7	30.6	28.4	25.2	31.2	26.2	21.0
P963 (R)	-	-	-	-	-	30.5	27.0	26.5	-	-	-	-	-	-
P9480 (R)	-	-	26.0	23.0	24.3	-	-	-	-	-	-	-	-	-
P9346 (R)	26.0	19.0	26.4	21.4	21.6	27.0	26.1	24.4	30.5	27.3	23.0	30.4	24.6	-

Table 5. Lower cheek teeth measurements of *Kolopsis yperus*. L = length; W = width; WP = width protolophid; WH = width hypolophid.

		P$_3$		M$_1$			M$_2$			M$_3$			M$_4$	
	L	W	L	WP	WP	L	WP	WH	L	WP	WH	L	WP	WH
P9483 (R)	-	-	-	-	-	-	21.0	-	29.0	23.9	21.5	30.9	25.0	20.0
P966 (L)	-	-	-	-	-	31.5	-	-	32.8	-	21.5	32.5	22.5	20.5
P9433 (L)	-	-	-	-	-	26.5	21.0	22.0	30.7	25.0	21.5	30.2	23.9	21.0

Table 6. Dimensions of *Kolopsis yperus* dentaries. * indicates approximation.

	P9433 (L)	**P9433** (R)	**P9483**	**P966**	**P9233**
depth of horizontal ramus below M$_{3/4}$	63.0	60.0*	66.6	55.0	60.0*
depth of horizontal ramus below M$_{1/2}$	50.5	-	53.0	-	76.0*
alveolar length, P$_3$ to M$_4$	135.2	-	142.0	128.5	132.0
thickness of symphysis	32.5	-	28.2	34.0	40.0
length mental foramen (?MEF) to masseteric fossa (?MAF)	168.0	-	152.5	-	174.5
thickness of coronoid (?COR) at postalveolar shelf (?PAS)	41.4	33.0*	37.0	41.0*	48.0

than the small oval metacone. A shallow labial crease extending from the mesostyle to the apex of the parametacrista corresponds to the division of the paracone and metacone. The mesostyle is a small, irregularly-shaped enamel crest composed of two small cuspules situated immediately anterior to a short, oblique posterolabial cingulum.

The P^3 of P961 is similar in overall shape to P9236 though larger, with much thicker enamel and deeper sulci between the cusps. The crown is heavily worn, exposing dentine on all cusps. The edges of the worn enamel crests are slightly rounded and less crisply defined than on the adjacent molar lophs. The parastyle, which is proportionally narrower transversely than that of P9236, is situated close to the base of the paracone. The lingual crest of the parastyle is more distinct than the labial crest and the tranverse sulcus is deeper lingually than labially.

The protocone is large and bulbous, being separated from the base of the parametacone by deep anteroposteriorly trending clefts extending from the middle of the transverse link. A shallow fossa, less distinct than in P9236, is present on the lingual side of the parametacone. The paracone is larger than the metacone which is separated by about 6.5 mm from the latter by a broad, shallow labial sulcus.The mesostyle is composed of a low enamel shelf from which a small cuspule arises, separating a shallow labial basin into two parts.

The P^3 of P9346 is more elongated than that of P961, but is neither as wide nor as thickly enamelled. Because P9346 was recovered before P961, the substantial differences in the size and morphology of the crown from that of the type specimen of *K. yperus* raised the possibility that it might represent another species. In particular, the narrow, elongated crown bears a striking resemblance to the P^3 of *Plaisiodon*

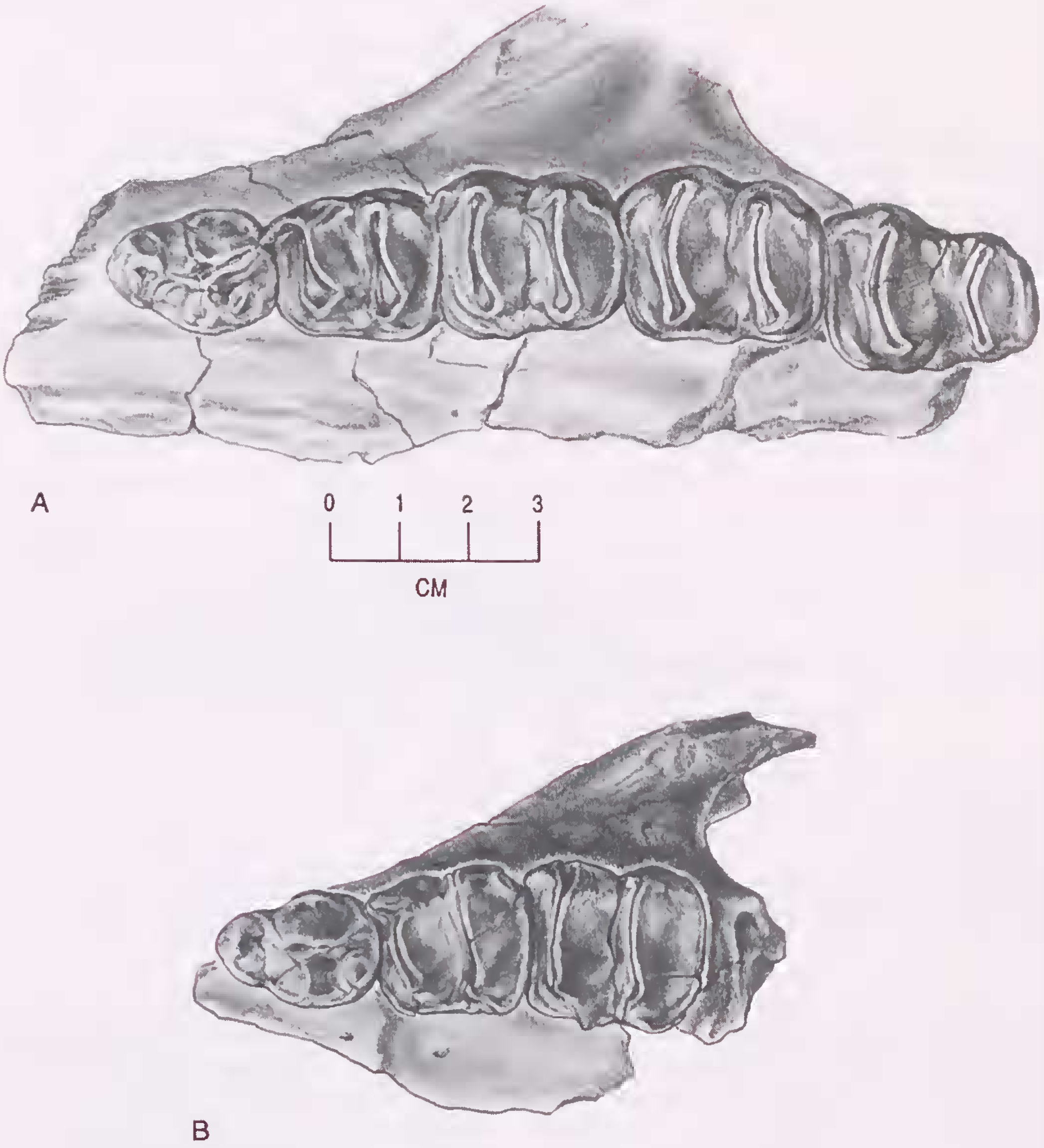

Fig. 10. Occlusal views of left cheek tooth rows of *Kolopsis yperus*. A, P961; B, P9236.

centralis. However, since *Plaisiodon centralis* consistently lacks any trace of a mesostyle or a labial crest on the parastyle, both of which are well-developed on P9346, the tooth cannot be allocated to that species either. The subsequent recovery of additional specimens closed the morphological gap sufficiently to confidently place the specimen within *K. yperus* as a rather extreme morphological variant. While the observed range of variation in the P³ morphology of *K. yperus* is in accord with the extent of variability encountered in other zygomaturine species for which a population sample is available, had we not found any intermediate specimens, its status would probably have remained dubious.

As in other specimens of *K. yperus*, the parastyle of P9346 is large and pressed close to the base of the paracone. The transverse sulcus is deep on both sides of the parastyle, meeting the labial and lingual ascending crests. The anterior profile of the parastyle is concavoconvex with a prominent basal expansion giving way to the slightly recurved tip. A large tear-drop shaped dentine exposure dominates the paracone. A faint secondary expansion of the enamel crests at the posterior end of the exposure probably

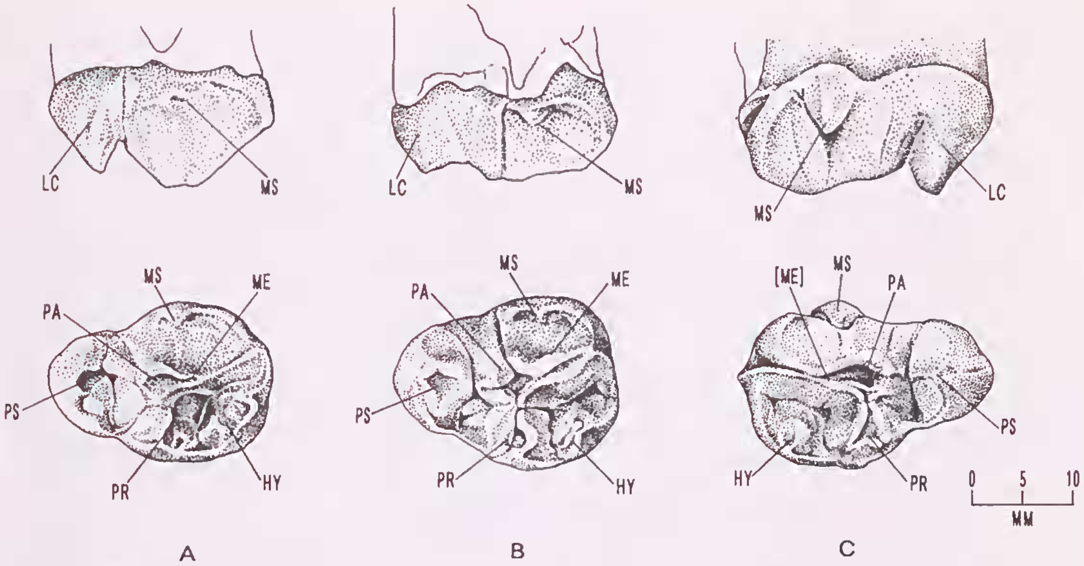

Fig. 11. P^3 specimens of *Kolopsis yperus*. **A**, P9236 left, labial and occlusal views; **B**, P961, left, labial and occlusal views; **C**, P9346, right, labial and occlusal views. Abbreviations: **HY**, hypocone; **LC**, labial crest of parastyle; **MS**, mesostyle; **PA**, paracone; **PR**, protocone; **PS**, parastyle.

represents the metacone, which is separated from the paracone by a faint labial groove. The mesostyle is a large triangular point of enamel isolated from the posterolabial cingulum by a V-shaped groove.

Upper molars. The molar row is curved (e.g. Fig. 10). The molars decrease in size in the order M^3, M^4, M^2, M^1. The M^1 crown is nearly rectangular, though slightly longer labially than lingually. The labial sides of the two moieties bulge prominently over the roots. The lingual side of the lophs are considerably higher than the labial side. The median valley is wide and open lingually but partially occluded labially by the postparacrista. There is no labial cingulum or mesostyle present.

The protoloph is strongly bowed anteriorly with a transversely narrow crest emarginating its deeply excavated posterior face. The metaloph is less curved and transversely much wider. The lingual side of the protocone slants into the loph, accentuating a wide expanse of the cingulum on the anterolingual corner of the crown. The posterior base of the protocone presents a flattened triangular facet, from which a low, oblique crest arises, extending from the apex of the protocone to the interloph sulcus. The labial side of the posterior fossa of the protoloph is formed by a low but distinct postparacrista. The parastyle is a large crescentic cuspule originating from immediately below and slightly lingual to the paracone, extending anteriorly to meet the base of the postmetacrista of the P^3 and forming a composite shearing crest.

The precingulum is thick and wide, expanding anterolingually around the base of the protocone where it merges with the lingual cingulum. The lingual cingulum expands slightly around the mouth of the interloph valley, emarginating a shallow interloph basin, then ascends the base of the hypocone a short distance, where it terminates. The postcingulum originates in a vertical crest extending about half-way up the posterolingual side of the hypocone. Expanding lingually near the base of the hypocone, the postcingulum continues around the base of the posterior facet of the metaloph to merge with a large crescentic metastyle on the labial corner of the P^3 crown.

The M^2 is much larger than M^1 and more uniformly rectangular in occlusal outline. The protoloph and metaloph are of about equal transverse width. The protoloph is less curved than in M^1 and the posterior face is not as confined or as deeply concave. The parastyle is smaller and situated lower on the precingulum. The precingulum extends lingually to the anterolingual side of the protocone base where it terminates, after ascending the side of the protocone a short distance. The lingual cingulum commences as a shelf-like emargination of the mouth of the interloph valley, terminating on the anterolingual side of the hypocone. The postcingulum originates from the posterolingual side of the hypocone, continuing around the base of the posterior facet of the metaloph to meet the low elliptical, swelling of the metastyle. The postparacrista is reduced to a low enamel bulge above the interloph sulcus at the base of the paracone. A short, weak labial cingulum is present in the mouth of the interloph valley.

M^3 is longer and asymmetrical, in that the metaloph is more obliquely oriented than the protoloph. Although the crests of the protoloph and metaloph are about equal in transverse width, the basal width of the anterior moiety greatly exceeds that of the posterior face. The parastyle is reduced to a small expansion of the precingulum. The interloph valley is much wider than in M^2 and the lingual cingulum is weaker, though similar in extent to that of M^2. The M^3 metastyle is about half the size of the M^2 metastyle and is located low on the posterolabial corner of the postcingulum. The lingual side of the postcingulum terminates on the posterior side of the base of the hypocone, and does not ascend the cusp as in M^2 and M^1.

M^4 is similar to M^3 except for its smaller size and much narrower metaloph. A small parastyle is present on the anterolabial corner of the precingulum. The metastyle is absent. A faint labial cingulum extends across the median valley mouth. The lingual cingulum is like that of the preceeding molar.

Mandible. Three similarly preserved hemimandibles are missing the lower incisor, P$_3$, M$_{1-2}$ and the posterior part of the horizontal ramus including the posterior masseteric eminence and the angular process. A fourth specimen represents a fragment of the posterior part of the ramus from which the molars are missing. These are more heavily constructed and in particular, much thicker in section and less sinuous in their profile than the equivalent element of *Kolopsis torus*.

The dentaries (e.g. Figs 12 - 14) are fully ankylosed at the symphysis and are broken on either the medial or lateral side of the median symphyseal crest. The horizontal rami taper gradually towards the symphysis, the profile of the inferior border ranging from slightly to moderately convex. The digastric process is fairly distinct, though low and rounded, being accentuated posteriorly by a broad, shallow postdigastric sulcus. The inferior border of the horizontal ramus is thick, though bordered ventrally by a sharp crest extending forward from the digastric process to the outer margins of large, deep genial fossae. The genial fossae are paired crescentic pits, separated by a low median crest. These extend across the entire ventral surface of the posterior margin of the symphysis.

The symphysis is massively thick and elongated. The ventral surface is horizontal while the dorsal surface slants upwards to form a U-shaped sublingual sulcus. The root fragment preserved in P9223 indicates that the lower incisors were procumbent to about the same degree as in *K. torus*. The round mental foramen is large on all specimens, opening anteriorly about 20.0 mm below the alveolar margin of the P$_3$ root within a shallow, oval subalveolar fossa.

The lateral surface of the horizontal ramus becomes strongly convex immediately behind the fossa, then flattens and narrows slightly at the transition to the ascending ramus. The masseteric fossa is moderately deep. A small masseteric foramen is present in three of the specimens and may be obscured by damage to the area in the fourth individual. The submasseteric crest is strong but the postmasseteric eminences and angular processes are missing on all specimens.

The intercoronoid sulcus is conspicuous for its considerable width, and the base of the coronoid crest is particularly massive. A shallow 10.0 mm diameter basin is contained within the postalveolar shelf. The postalveolar process, represented by a low tubercle or thickening of the margin of the postalveolar shelf, is weakly developed on all specimens.

The digastric fossa tapers anteriorly to the level of interproximal M$_2$/M$_3$. It is deepest and widest at the level of the posterior root of M$_4$. The pterygoid fossa is confluent with the digastric fossa, though a faint crest indicates a definite separation of the two structures. The alveolar protuberance of the last two molars is massive and overhangs the digastric fossa by as much as a centimetre in P9344.

The markedly tangential orientation of the cheek tooth rows of this species results in a considerable overhang of the alveolar margins by the protolophid of M$_2$ and the hypolophid of M$_4$. A considerable range in size and basic shape of the dentaries is evinced by the Ongeva sample, suggestive of sexual dimorphism. P9483 and P9344 are smaller, more slender and have straighter ventral profiles of the horizontal rami than P966 and P9223.

Lower molars. The lower premolar and first molar are not known for this species. Molars 2-

4 are essentially alike, their length and width gradually increasing posteriorly. The lower molars are relatively broad and rectangular, with thick enamel and wide, robust lophids. The interlophid valleys are wide and U-shaped in labial aspect. On all molars the hypolophids are more curved and transversely narrower than the protolophids. The precingulids are weak and confined to the labial and lingual corners of the base of the protolophid. The postcingulid projects posteriorly in the form of a narrow, rounded shelf with a slight elevation below the middle of the hypolophid. A low metalophid is present on the last two molars, being more strongly expressed on M_4.

Systematic considerations. An indication of P^3 size range in *K. yperus* is provided by the new material. The type *K. yperus* P^3 is smaller than that of the *Zygomaturus gilli* type by 2.0 mm of length and 0.3 mm of width. The largest of the new specimens exceeds the P^3 length of *Z. gilli* by 4.5 mm. The degree of variability in *K. yperus* (comparable to that observed in other zygomaturine species) encompasses that of the sole specimen of *Z. gilli*, which, when combined with a morphological similarity, substantially increases the likelihood noted by Murray *et al.* (1993) that the two taxa are synonymous. However, more specimens are needed of *Z. gilli*, including the M^1, before a synonymy can be objectively established.

While *Zygomaturus gilli* has taxonomic priority over *Kolopsis yperus*, generic distinctions within the Zygomaturinae may require redefinition if they are to meaningfully reflect hypotheses of evolution in the group and express their biochronological utility. The morphological similarity of *K. yperus* and *Z. gilli* indicates that they are at a similar stage of evolution.

The basic structural progression from *Neohelos* to *Kolopsis* to *Zygomaturus* was originally outlined by Stirton *et al.* (1967). The geno-

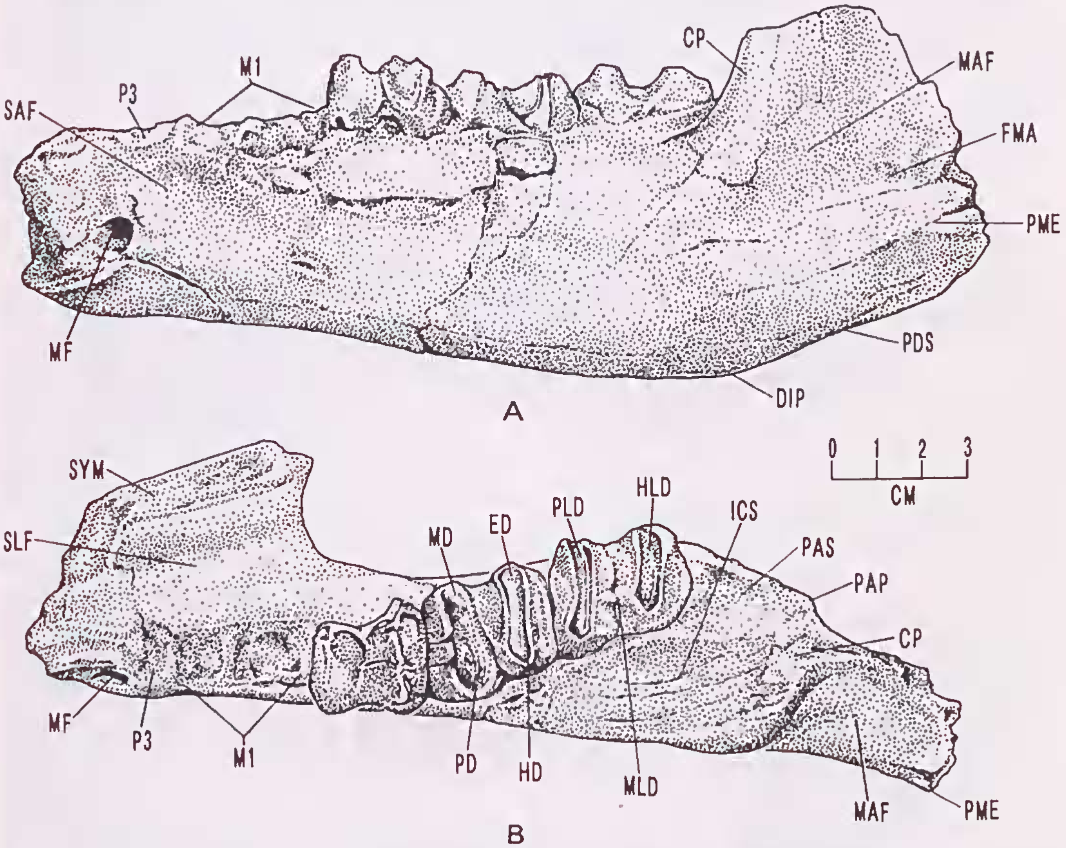

Fig. 12. Left dentary of *Kolopsis yperus* (P9344). A, lateral aspect; B, occlusal aspect. Abbreviations: **M1**, first lower molar; **CP**, anterior crest of coronoid process; **DIP**, digastric process; **ED**, entoconid; **FMA**, masseteric foramen; **HD**, hypoconid; **HLD**, hypolophid; **ICS** intercoronoid sulcus; **MAF**, masseteric fossa; **MD**, metaconid; **MF**, mental foramen; **MLD**, metalophid; **P3**, lower permanent premolar; **PAP**, post-alveolar process; **PAS**, post-alveolar shelf; **PD**, protoconid; **PDS**, post-digastric sulcus; **PLD**, protolophid; **PME**, posterior massteric eminence; **SAF**, subalveolar fossa; **SLF**, sublingual fossa; **SYM**, symphysis.

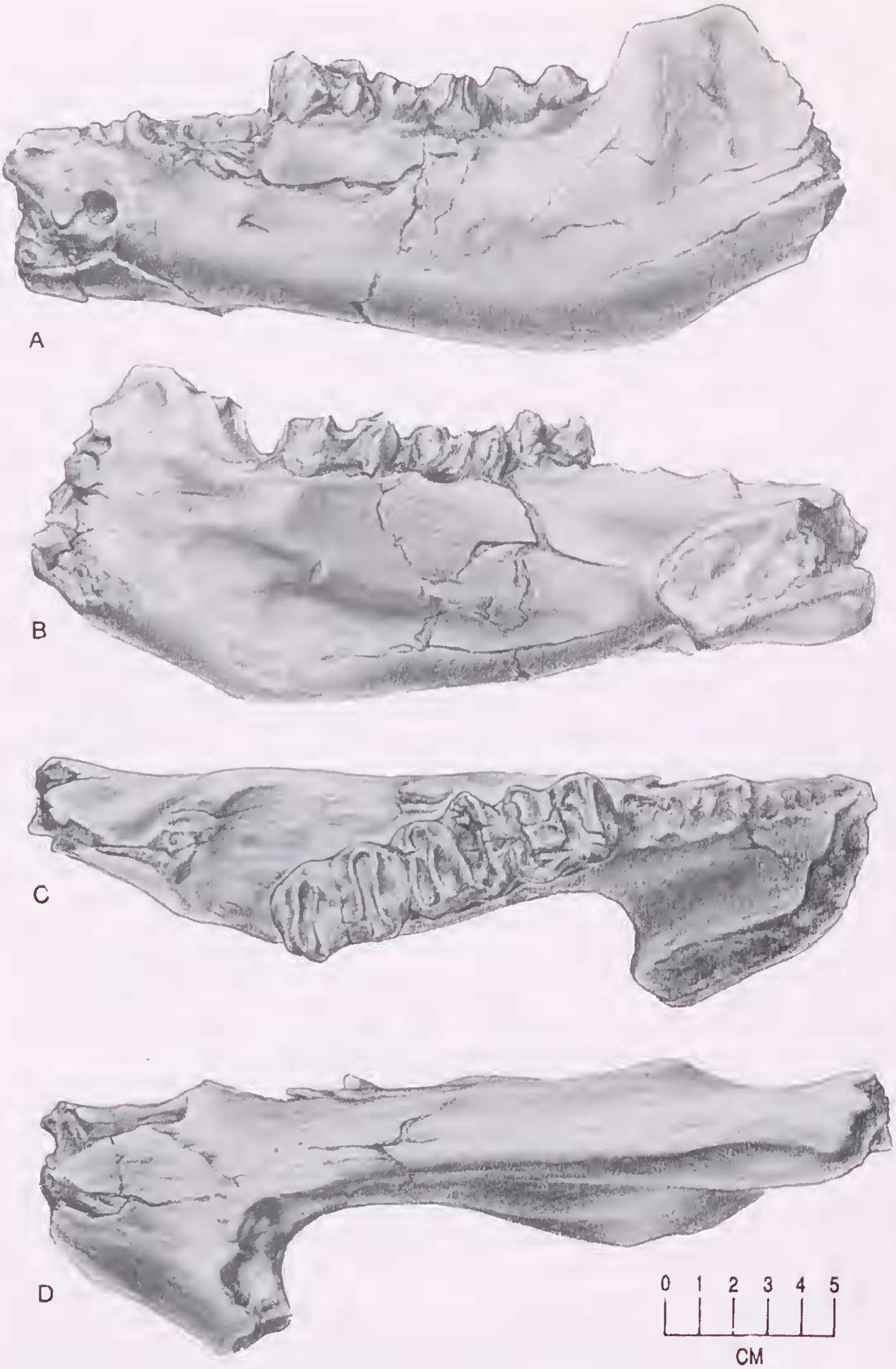

Fig. 13. Left dentary of *Kolopsis yperus*, NTM P9344, note slender horizontal ramus and straight inferior border. **A**, lateral aspect; **B**, internal aspect; **C**, occlusal aspect; **D**, ventral aspect.

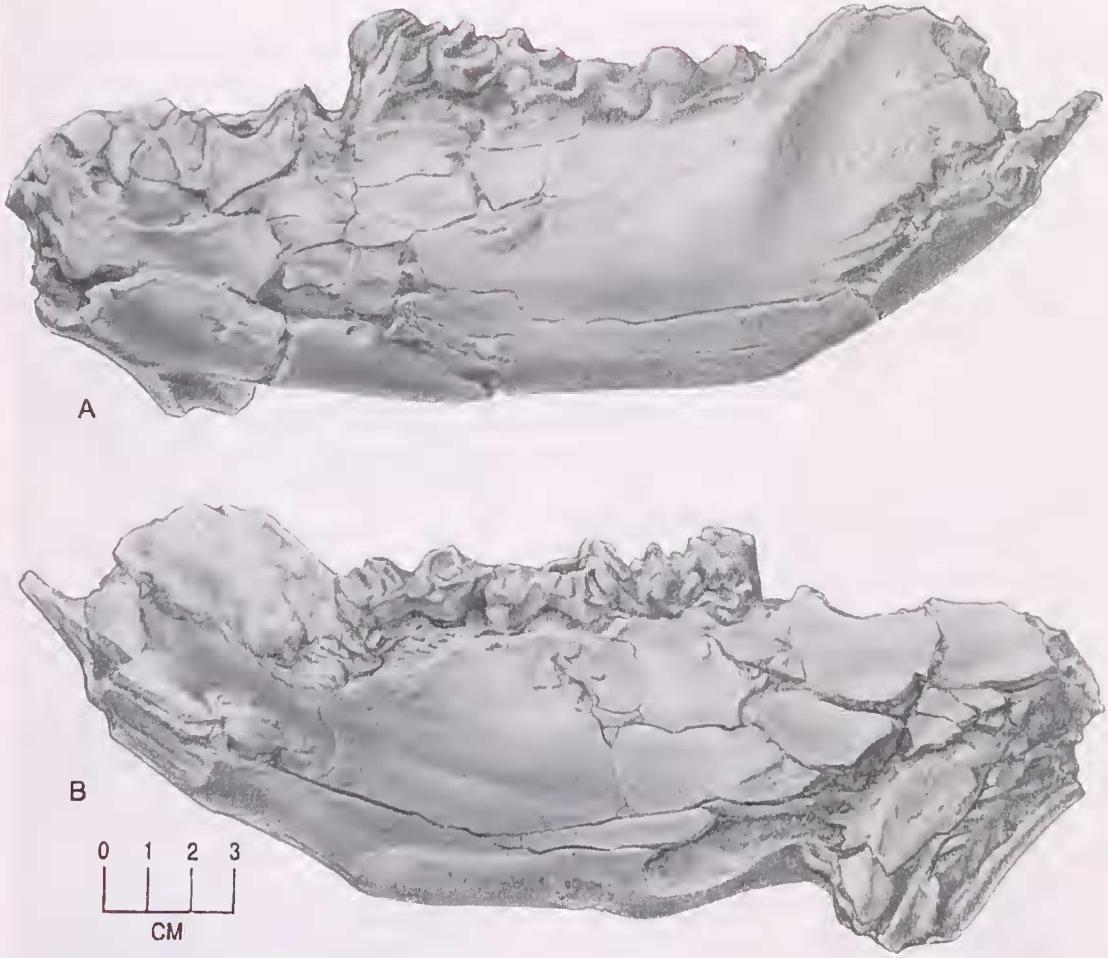

Fig. 14. Left dentary of *Kolopsis yperus*, P966; an example of the larger, deeper specimens with a rocker-shaped inferior profile. A, lateral aspect; B, internal aspect.

typic (and in 1967, the only known) species of *Neohelos* and *Kolopsis* expressed degrees of morphological difference from each other, and from previously described species of *Zygomaturus*, that warranted generic distinction. Subsequently described species have closed the gaps between genotypes, so that generic classification now subdivides what appears to be a successional spectrum.

Stirton (1967) had no difficulty in placing *keanei* with other species of *Zygomaturus*, but placed *gilli* in the same genus with reservations. Murray (1992) also expressed reservations about its placement.

Primitively (as expressed in early and mid Miocene species of *Neohelos*), the P^3 parametacone is expressed as a single cusp. Incipient division of the cusp first appears in the mid Miocene in an undescribed new species of the genus *Neohelos* (Murray *et al.* in prep.). A clear and consistent division of the cusp is a shared derived character state of late Miocene and younger zygomaturines placed in *Kolopsis*, *Zygomaturus*, *Maokapia* Flannery, and *Hulitherium* Flannery and Plane. Taxonomic distinctions and subdivision of this clade using dental characters, however, relies on the upper molars as well, especially the M^1.

In an attempt to use the established nomenclature in a manner that reflects both morphology, hypotheses of relationship, and stratigraphic succession, we follow Murray (1992) in recognising the genus *Kolopsis* as: species possessing elongated P^3 with consistently and distinctively divided parametacone, P^3 crown approximately equal in length to M^1 crown; M^1 with large parastyle forming functional shearing crest with the postmetacrista of P^3; and the genus *Zygomaturus* as species possessing short, broad P^3 with divided parametacone, crown significantly reduced in size relative to M^1; M^1 parastyle reduced, resulting in diminished shearing function and squaring of occlusal outline.

According to these definitions, *gilli* groups with *Kolopsis* on the basis of P^3 morphology, but what is not known of *gilli* is the state of the M^1 parastyle, and the size of P^3 relative to M^1. Other *Zygomaturus* spp., *Maokapia* and *Hulitherium* are derived with respect to *Kolopsis* in shortening and broadening of the P^3, and the P^3 reduced in size relative to M^1. These character states (amongst a much larger suite of derived dental and cranial characters) were used by Murray (1992) to define a clade, the Zygomaturini, which is a crown group based in the mid Pliocene on *Z. keanei*.

There remains within this model and scope of this work the question of which of *Kolopsis torus* or *Kolopsis yperus* most likely gave rise to *Z. keanei* and its descendents. As these *Kolopsis* species coexist in the Ongeva Local Fauna, they must share an ancestor. The new *Neohelos* species mentioned above has no character states that preclude it from ancestry of either species. The molars of *K. torus* are practically indistinguishable in size and morphology from this. However, the P^3 crown is substantially reduced in height and also relatively much lower in comparison with all species in the *Z. keanei* crown group. A reduced P^3 crown thus may represent an autapomorphy of *Kolopsis torus*. On the other hand, *Kolopsis yperus* retains a high-crowned P^3 similar in proportion, though larger than that of the advanced *Neohelos* species, and therefore is more plausible as an ancestor of *Zygomaturus keanei* (Fig. 15).

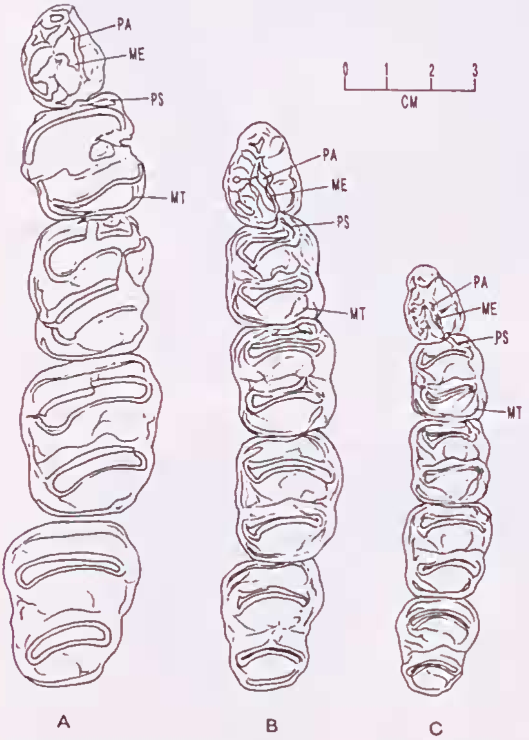

Fig. 15. Scale comparison of the cheek tooth rows of: A, *Zygomaturus keanei* Stirton; B, *Kolopsis yperus*; and C, *Kolopsis torus*. *Z. keanei* after Stirton (1967: fig. 2).

Any formal taxonomic revisions, however, should wait until descriptions of new zygomaturine species are published (B. MacNess pers comm.; Murray *et al.* in prep.), and hypotheses of relationships tested further.

Eusuchia Huxley
Crocodylia Gmelin
Crocodylidae Cuvier
Quinkana Molnar
species indet.
(Figs 16-18, Table 7)

Material. NTM P9229, right dentary fragment preserving five partial alveoli; P9226, P9227, P9230, and P91163-(12 to 21), osteoderms; P91163-(1 to 4), and P9232-(1 to 11), laterally compressed tooth crowns.

Description. The structure of the right dentary fragment, NTM P9229, is shown in Figure 16. The fragment represents the posterior portion of dentary in the vicinity of the foramen for the Ramus intermandibularis medius (a branch of the trigeminal nerve), visible in medial view, and opening through the lateral wall of the primordial canal of the mandible.

The most striking feature of the fragment is a massive, laterally-projecting longitudinal crest along the dorsolateral margin of the dentary ramus. Sculpture is most strongly developed on the lateral face, but continues over the crest and around onto the ventral surface, where its expression is more subdued. Laterally, the sculpture is dominated by marked ridges and sulci, with several large nutrient foramina opening posteriorly. Ridges and sulci are also present on the ventrolateral crest, but augmented by numerous, small, rounded pits. Ventrally, the ridges and sulci are greatly subdued, the pits are smaller but more numerous, and the result is an almost granular surface texture.

Five partial, closely-approximated alveoli are represented. In dorsal view, the alveoli are longer (antero-posterior dimension) than they would have been wide when complete (transverse dimension). In slightly dorsolateral view it is apparent that the long axes of the more complete alveoli are inclined, rather than parallel, to the lateral margin of the dentary. The anterior alveoli are slightly larger than the two most posterior ones, but the size difference is not large, suggesting an animal with a rather isodont dentition.

The isolated tooth crowns are laterally compressed and recurved (Fig. 17, Table 8), with prominent anterior and posterior carinae. Many of the crowns flare medially near the base, resulting in basal width (transverse dimension) to length (anteroposterior dimension) ratios that are greater than at more distal parts of the crown. The Ongeva teeth show relatively little variation in size and proportions, and while it impos-

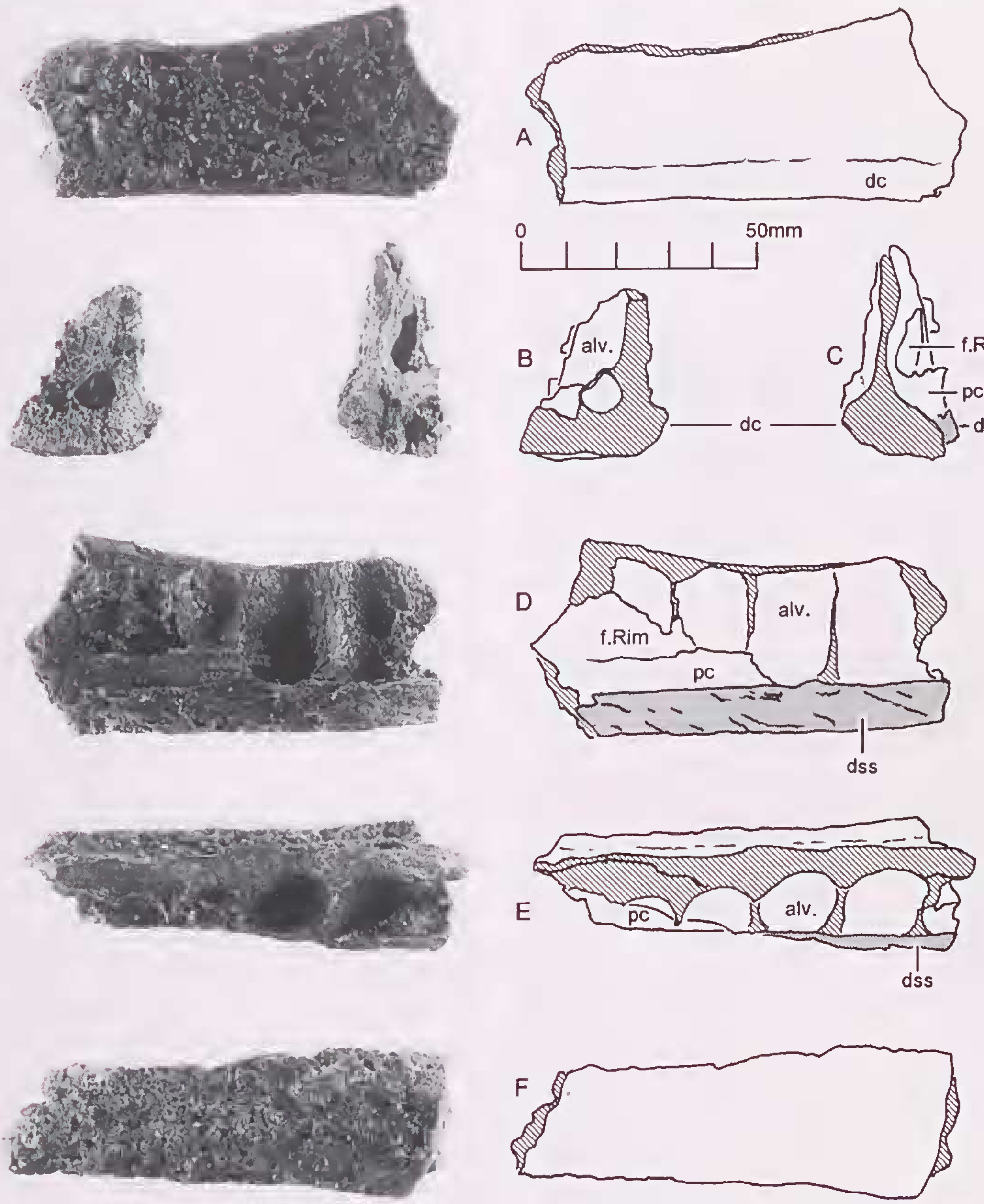

Fig. 16. Ongeva Local Fauna *Quinkana* sp. dentary fragment P92229 in **A**, right lateral; **B**, anterior; **C**, posterior; **D**, medial; **E**, dorsal and **F** ventral. Abbreviations: **alv.**, alveolus; **dc**, dentary crest; **dss**, dentary-splenial suture; **f.Rim**, foramen for the Ramus intermandibularis medius; **pc**, primordial canal of the mandible.

sible to ascertain the number of individuals that might be represented, or where in the dentition the individual teeth came from, the sample also suggests that a species with a rather isodont dentition is present. For most teeth, preservation is such that microscopic features of the carinae are no longer discernible. However, on P91163-4, P9232-3 and P9232-5, segments of the carinae retain fine, evenly spaced serrations (ca. 6 or 7 per mm).

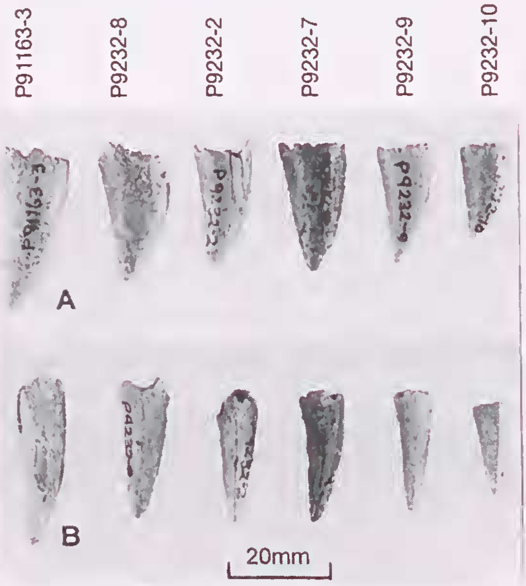

Fig. 17. A selection of *Quinkana* sp. teeth in A, lateral and B, anterior or posterior views.

The osteoderms are variously of rectangular to irregular outline (Fig. 18). Medial crests are very weakly to strongly developed. The sculpture consists predominently of anastomosing ridgelets bounding irregular pits, or sulci radiating from the medial crests. Some have a dorsal, anterior flattened area where they imbricated with the adjacent anterior osteoderm, and/or a corresponding ventral posterior articulating surface. Typically, one or both lateral edges preserve sutures. The variety of shapes, degree of crest development, and distribution of sutural and imbricating surfaces suggests that dorsal armour from various regions of the trunk are represented.

Comparative remarks. The dentary fragment retains several characters diagnostic of the two known species of *Quinkana*, *Q. fortirostrum* Molnar, 1981, and *Q. timara* Megirian, 1994. These include alveolar morphology indicative of a closely approximated, relatively isodont dentition, laterally compressed teeth, and long (anteroposterior) axes of the teeth inclined to the lateral margin of the dentary ramus. A ventrolateral crest on the dentary ramus is known to occur in *Quinkana timara*, but no comparable *Q. fortirostrum* material is known.

The associated Ongeva Local Fauna teeth are consistent in their morphology with the dentary

Table 7. Morphometrics of Ongeva Local Fauna *Quinkana* sp. teeth, compared with *Q. timara* (Megirian 1993: Table 2), and Croyden *Quinkana* sp. (after Molnar 1981: Table 2). Dimensions in mm; bracketed figures are estimates.

Specimen	Length 'L'	Width 'W'	Height 'H'	W/L	Serrations per 5mm (approx.)
P91163-1	[14.2]	[10.4]	[32.5]	[0.73]	-
P91163-2	[13.7]	-	[25.5]	-	-
P91163-3	13.7	[10.0]	34.3	0.73	-
P91163-4	-	-	>23.5	-	30
P9232-1	10.3	7.0	23.3	0.68	-
P9232-2	11.7	[8.3]	26.6	[0.71]	-
P9232-3	-	11.9	30.6	-	30
P9232-4	10.5	7.2	21.4	0.69	-
P9232-5	-	-	31.8	-	35
P9232-6	12.2	9.6	24.5	0.79	-
P9232-7	13.7	9.2	26.3	0.67	-
P9232-8	[14.7]	[10.3]	28.5	0.70	-
P9232-9	10.8	7.6	24.1	0.70	-
P9232-10	10.2	7.3	18.7	0.72	-
P9232-11	-	-	>26.4	-	-
Range					
Ongeva LF *Quinkana* sp.	10.2 -14.7	7.0 -11.9	18.7 -34.3	0.68-0.79	30 -35
Q. timara (n = 14)	5.3 - 9.2	2.2 - 5.0	3.5 -14.4	0.37-0.79	35 -50
Croydon *Quinkana* sp. (n = 4)	8.0 -11.0	4.4 -10.3	-	0.54-0.64	18 -27

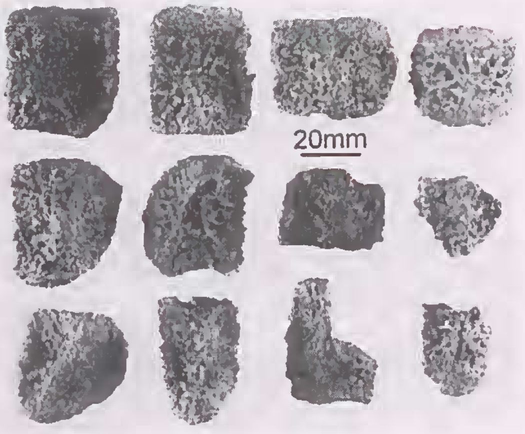

Fig. 18. A selection of osteoderms, in dorsal view, assigned to *Quinkana* sp.

alveoli, but are not as compressed as the most extreme examples of *Q. timara*. They correspond to the higher width to length ratios recorded for *Q. timara*, and are slightly less compressed than Pliocene *Quinkana* sp. specimens from Croydon, Queensland (Table 7). Many of the Ongeva Local Fauna teeth flare medially near the base, resulting in basal width to length ratios that are somewhat higher than along the rest of the crown. The frequency of serrations of Ongeva Local Fauna teeth are equal to, or lower, than in *Q. timara*, but higher than in Croydon *Quinkana* sp. The sole specimen of *Quinkana fortirostrum* is edentulous. A species determination is not possible on the basis of the available material.

Osteoderms are of little diagnostic value in distinguishing Australian fossil taxa at this stage, as no detailed comparative studies have been made. Megirian *et al.* (1991: fig. 8) illustrated two osteoderms included in *Harpacochampsa camfieldensis* which differ from the Ongeva osteoderms in having circular pits rather than ridges and sulci. The Ongeva Local Fauna osteoderms are provisionally assigned to *Quinkana* sp. on the basis of association and the present lack of any evidence of another crocodilian taxon at the Ongeva locality.

PALAEOENVIRONMENTAL RECONSTRUCTION AND FAUNAL SUCCESSION

Murray and Megirian (1992) contrasted the central Australian Alcoota LF (late Miocene) with the mid Miocene Bullock Creek Local Fauna from the north central Northern Territory. For practical reasons, only a selection of material from each assemblage was chosen for analysis, and while various calculations were presented on such things as relative abundances, the approach used was descriptive, with any calculations merely illustrating qualitative differences. The approach was intended to facilitate a first order approximation of '...the pattern of succession, the factors of mortality, the similarities and differences in community structure, [and] the shared and contrasting palaeoenvironmental factors ...' (Murray and Megirian 1992: 195). A similar approach is used here to compare the two Waite Formation assemblages, and as with the earlier work (Murray and Megirian 1992), it is hoped that more rigourous methods can be applied in the future.

The Ongeva LF beds contain fossils in significantly lower concentrations than was found in the Alcoota LF beds. Recovery of the Ongeva LF is further limited by the large overburdens that accompany excavating into the steep sides of Hill 1. On the other hand, the Alcoota LF beds are very rich and relatively extensive beneath a surface of low relief. Large quarries have been developed by the removal of overburden by heavy machinery. In terms of future prospects, the Ongeva quarries will probably never produce the quality and range of material, and taxonomic diversity already recovered from the Alcoota quarries. Quarrying on Hill 1 will continue with the primary objective of recovering diagnostic material of forms already known to be present in the Ongeva LF, and hopefully, additional taxa. Although the following comparisons are based on unequal samples, the differences in the incidences of certain species and the total absence of others suggests that the two faunas sample somewhat different communities.

The Ongeva LF is considerably less diverse than the Alcoota LF (Table 8). Both faunas are dominated by large herbivores, notably diprotodontids and dromornithids. Based on preliminary identification of the Ongeva dromornithids, both faunas contain (cf.) *Genyornis* and (cf.) *Ilbandornis*. At the specific level they share only *Kolopsis torus*: the Alcoota LF contains several diprotodontid herbivores not represented in the Ongeva LF (*Alkwertatherium*, *Palorchestes*, *Pyramios*, and *Plaisiodon*), while *K. yperus* is unique to the Ongeva LF.

In the Alcoota Local Fauna, *K. torus* and *Plaisiodon centralis* are closely associated by

Table 8. Comparison of the Alcoota and Ongeva Local Faunas. Alcoota LF after Murray and Megirian (1992: Table 2).

		Alcoota LF	Ongeva LF
MOLLUSCA	Gastropoda	undetermined	-
REPTILIA	Chelidae	undetermined	-
	Crocodylidae	*Baru* cf. *darrowi*	-
		-	*Quinkana* sp.
	Varanidae	?*Megalania*	-
AVES	Casuaridae	*Dromaius* sp.	-
	Dromornithidae	*Dromornis stirtoni*	cf. *Dromornis*
		Ilbandornis lawsoni	cf. *Ilbandornis*
		Ilbandornis woodburnei	
	Anatidae	undetermined	-
	Accipiteridae	undetermined	-
	Phoenicopteridae	undetermined	-
MAMMALIA	?Peramelomorphia	undetermined	-
	?Dasyuridae	undetermined	-
	Thylacinidae	*Thylacinus potens*	-
	Thylacoleonidae	*Wakaleo alcootensis*	-
	Vombatidae	undetermined	-
	Diprotodontidae	*Pyramios alcootense*	-
		Alkwertatherium webbi	-
		Plaisiodon centralis	-
		Kolopsis torus	*Kolopsis torus*
		-	*Kolopsis yperus*
	Palorchestidae	*Palorchestes painei*	-
	Petauridae	*Pseudocheirops* sp.	-
	Macropodidae	*Hadronomas puckridgi*	-
		Dorcopsoides fossilis	cf. *Dorcopsoides*
		cf. *Dorcopsoides*	-
		Protemnodon sp.	-

virtue of their respective relatively high frequencies in the assemblage, so the apparent absence of *P. centralis* in the Ongeva LF is noteworthy. In terms of size and dentition, *K. yperus* and *P. centralis* are very similar and possibly occupied similar ecological niches, suggesting that (locally at least) the former species displaced the latter. A similar association between a large and small zygomaturine appears to have existed at Beaumaris, Victoria, where *Zygomaturus gilli* is found in association with a closely related but much smaller species. The small Beaumaris species is distinct from *Kolopsis torus* in having narrower molars, but could, as suggested by Rich (1976), represent another species of *Kolopsis*. The significance of these associations and possible successions are not understood, but might be related to the persistence of certain habitats adjacent to, or within, other more extensive regions undergoing rapid environmental change.

Of the taxa occurring at lower frequencies in the Ongeva LF, a small macropodid (cf. *Dorcopsoides*) is shared with the Alcoota LF. More generally, small animals are more poorly represented in the Ongeva LF than they are in the Alcoota LF. The ziphodont crocodylid, *Quinkana,* has not yet been determined in the Alcoota LF, and conversely *Baru* has not yet been determined in the Ongeva LF. Aquatic animals are rare in the Alcoota LF, and unknown in the Ongeva LF if one accepts *Quinkana* as a crocodylid adapted for life on land (Megirian 1994).

The Alcoota thanatocoenosis is characterised by intact bones showing little or no evidence of pre-burial weathering, a large number of individuals represented by associated skeletal elements (occasionally in partial articulation), short transport and rapid burial, and a notably high diversity of diprotodontid marsupials compared to any other Neogene assemblages. Murray and Megirian (1992) attributed mortality to a specific event, water-hole tethering during a drought, with subsequent rapid burial resulting from a drought-breaking flood, or several such close-spaced events, which mobilised large amounts of sediment and dumped it as poorly sorted, poorly bedded braided deposits. The local 'water-hole' was interpreted to be a lake, or series of small lakes some relatively short distance downstream from the fossil accumulation. The aquatic components of the Alcoota LF suffered less during the drought (as evidenced by the low frequency of skeletal remains), retreating with the lake waters to lower parts of the basin. A general lack of evidence for bone damage due to predation and scavenging was attributed to a temporary imbalance of the predator / scavenger (secondary consumer) guild with respect to the congregated primary consumers.

The Ongeva sediments, deposited after at least two extended periods of non-deposition are, in general, coarser than the Alcoota LF beds, though also poorly sorted. They contain more angular particles. The channel in the Ongeva section is relatively deeply incised, and bedding contacts within the fossiliferous sequence more clearly defined. Compositionally, the sediments appear quite similar. Bones of the Ongeva LF are completely disassociated from their skeletons and show a greater range of pre-burial alteration than is typical for the Alcoota LF. Even the most robust skeletal elements, such as dentaries and maxillae of mammals, and leg bones of the giant flightless birds, are rarely complete.

Damage to the ends of long bones in the Ongeva LF may have resulted from predator or scavenger damage, trampling, destructive transport, or a combination of factors. The rounding of many broken edges is probably due to the effects of hydraulic traction. Primary evidence for trampling in the Alcoota LF consists of bones crushed only in places, with the crushed bone becoming buried *in situ*. No such preservation has been recorded in the Ongeva LF, but breakage due to trampling can be assumed from herbivore coprolites deposited directly upon bones. No unambiguous evidence for predator and scavenger damage can be presented on the available material which preserves little surface detail. Significant, though patchy, contribution of small bone shards to the matrix of fossiliferous strata is a feature of the Ongeva LF beds: no comparable concentrations have been observed in the Alcoota LF beds. Their presence in the Ongeva LF suggests that some animal skeletons lay exposed on the surface long enough for the breakdown of collagen before burial of the remains. Compared to the Alcoota LF, large bones are even more disproportionately represented relative to smaller skeletal elements, a feature attributable to winnowing.

Few specimens per individual, and few individuals, are required to account for the yield of diagnosable Ongeva LF material. For example, using only skull fragments and disregarding relative stages of tooth wear, three individuals could minimally account for *K. torus* (e.g. three left dentaries); five individuals could account for *K. yperus* (three adult right maxillae, the holotype P^3+M^1 which do not match any of the maxillae, and a dentary of a juvenile); and one individual accounts for *Quinkana* sp.

There is nothing in the Ongeva LF to suggest a community under the degree of environmental stress, specifically drought, that led to the Alcoota LF thanatocoenosis. The coprolites indicate that conditions were tolerable for herbivores. An analogy can be made with the consistency and consequent depositional form of domesticated bovid excreta which varies according to the feed available. Where feed is succulent, excreta dropped from anal height splatters widely around the point of impact. At the other extreme, where feed is very dry and coarse, excreta tends to be hard and pelletal, with pellets surviving their fall without deformation. The intermediate form has a coherence that results in a well-rounded, regular pat with concentric rippling. The Ongeva coprolites most closely resemble this intermediate form, suggesting by analogy with cows, that conditions at the time of deposition were favourable, though perhaps towards the drier end of the scale, for bulk-feeding herbivores. Associated cow-sized taxa possibly responsible for coprolite deposition are the herbivorous / seed-eating giant flightless bird cf. *Genyornis stirtoni*, or one of the diprotodontid marsupials (more likely *Kolopsis yperus*, but *K. torus* cannot be ruled out). (In 1995, a large pelletal coprolite was collected from the Alcoota LF.)

The sedimentology of the Ongeva LF beds indicates a relatively more proximal part of an alluvial system compared to the Alcoota LF beds. On Hill 1, fossiliferous sediments are confined to distinct channels with cobble conglomerate basal lag. On the other hand, in the Alcoota quarries fossils are contained in more poorly defined, probably braided, channel deposits (typically pebble grade at their base), and in adjacent finer sediments (sand and silt grade) that possibly represent lateral accretion facies. The relative energies in the two systems account for many of the differences in bone size, sorting, and whatever damage can be attributed to traction noted above

The Ongeva LF is most likely to have resulted from natural attrition about a possibly seasonally flowing stream channel. Presumably between foraging, the animals were drawn from the local environs to small, permanent or semi-permanent pools, but not under the duress of an extended drought.

CONCLUDING REMARKS

There is evidence in the Waite Formation at Alcoota of tectonism, possible changes in stream gradients and/or direction, coarsening upwards of sediments, and depositional hiatuses marked by the effects of deep weathering. While the Alcoota LF beds (predominantly siltstone and sandy siltstone) are generally finer than the stratigraphically higher beds at Hill 1, they too are poorly sorted and contain lenses and channel fills of coarse (to pebble size) material. Murray and Megirian (1992) suggested on sedimentological and palaeontological grounds that these sediments represent distal fluvial to marginal lacustrine facies of an intermontane basin. Coarser channel facies higher in the section reflect more proximal fluvial characteristics. Woodburne (1967a) characterised this transition by sub-dividing the Waite Formation into a lower 'lacustrine' member and a higher 'fluviatile' member. The overall coarsening upwards of the succession, as well as the drop in compositional and textural maturity across the boundary of units III and IV, could be explained by a change in sediment provenance (derivation from sources closer to the point of deposition), increase in hydraulic gradients (due perhaps to tectonism or lake regression), change to drier climate (less chemical weathering and mechanical abrasion of particles during hydraulic traction), or some combination of factors. If the correlations between outcrops of Waite Formation proposed by Woodburne (1967) are correct, then deposition of the Alcoota and Ongeva Local Faunas predate folding at Hill 3. The evidence presented in Senior *et al*. (1995) for reversed (relative to present) stream drainage in the Waite Formation at Utopia, north of the study area, cannot be directly linked to indications of a change in sediment provenance preserved on Hill 1. However, both sets of observations point to phenomena producing changes in basin drainage during Waite Formation times.

The differences between the Alcoota and Ongeva LFs result from taphonomic and preservational biases, a range of palaeoenvironmental factors, as well as morphological evolution and faunal turnover over an unknown length of time. The Ongeva assemblage is more likely to have resulted from natural attrition around waterholes in seasonally flowing rivers than from a mass mortality due to extended drought such as that postulated by Murray and Megirian (1992) to have produced the Alcoota Local Fauna. Of the Zygomaturinae, *Kolpsis yperus* makes its appearance in the Ongeva LF, and may have displaced *Plaisiodon centralis* from the Alcoota Local Fauna. On the other hand, *Kolpsis torus* persisted.

Murray *et al*. (1993) attached biochronological significance to *K. yperus*, arguing that consistent with superpositional relationships, it represented a stage-of-evolution slightly advanced over Alcoota LF *K. torus*, approaching that of *Z. gilli* (Beaumaris LF, Victoria). New *K. yperus* material indicates that this taxon is somewhat closer to *Z. gilli* from the Cheltenhamian Stage of Victoria than previously supposed by Murray *et al*. (1993), and the two may be synonymous. The age difference between the Alcoota and Ongeva LFs time does not appear to be great. *Kolopsis torus* persisted from Alcoota to Ongeva LF time, with so little morphological change that a distinction of morphospecies, or even sub-species, cannot be justified.

Whatever the causes of the differences between the Alcoota and Ongeva Local Faunas, the two are biostratigraphically distinct.

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It is not our intention in naming so few to diminish the contributions to this work of our many friends, volunteers, colleagues, Flinders University students, and hosts at Alcoota. Mick Whitelaw most generously placed his resources and expertise in palaeomagnetics at our disposal. Our thanks to all.

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